Middle-Late Miocene Spalacidae (Mammalia) From Western Anatolia, and the Phylogeny of the Family

Orta-Geç Miyosen Batı Anadolu Spalacidae (Mammalia) Fosillerinin Ailenin Evrimine Katkısı

*Şevket ŞEN[1], Nuran SARICA[2]

[1]CR2P-CNRS, Muséum National d'Histoire Naturelle, 75005 Paris, France.

[2]İstanbul Teknik Üniversitesi, Maden Fakültesi, Jeoloji Mühendisliği Bölümü, Ayazağa, 34469 İstanbul, Turkey.

ABSTRACT

The Spalacidae (Rodentia, Mammalia) are among the common elements of Neogene and Quaternary mammalian faunas in Turkey. Their evolutionary dynamics since the Early Miocene allows their use for dating Neogene and Quaternary terrestrial deposits. This paper describes spalacid fossils from three Middle-Late Miocene localities in Western Anatolia; two of them yielded two new species. To test the monophyly of the known genera and to establish phylogenetic relations of fossil species, a cladistic analysis has been performed. The enlightenment of their evolutionary trend towards adaptation to a fully subterraneous life required the analysis of the dental features of available and well-represented fossil species and the discussion of their phylogenetic relationships. It appears that the first representatives of the family originated in Anatolia during the Early Miocene, as suggested by previous studies, then rapidly dispersed into south-eastern Europe, and probably much later (?Pliocene) into southwest Asia and North Africa. Their representatives adapted to a fully subterraneous mode of life during the Late Miocene, when open environments prevailed in western Asia and SE Europe.

Key Words: Biostratigraphy, cladistic analysis, Miocene, phylogeny, Rodentia, Spalacidae, systematics, Turkey.

ÖZ

Köstebekler (Spalacidae (Rodentia, Mammalia) Türkiye'de Neojen ve Kuvaterner yaşlı faunalar içinde sıkça bulunanlardır. Erken Miyosen'den beri gösterdikleri güçlü evrim dinamiği nedeniyle, bu ailenin türleri Neojen ve Kuvaterner karasal tortulların yaşlandırılmasında başarılı olarak kullanılır. Bu yayında Batı Anadolu'da Orta-Geç Miyosen yaşlı üç lokasyonda bulunmuş Spalacidae fosilleri ve onların içerdiği iki yeni tür tanımlandı. Bu aileye katılan cinslerin tek kökenli olup olamadığını ve türler arasındaki evrimsel bağlantıları aramak için kladistik analiz yöntemi kullanıldı. Ailenin evrimsel sürecini ve yeraltı yaşamına uyma nedenlerini daha iyi anlamak amacıyla da bilinen bütün fosil türlerin diş yapıları incelendi. Elde edilen sonuçlar, Spalacidae ailesinin, daha önceki çalışmalarda da belirtildiği

Ş.Şen
E-mail: sen@mnhn.fr

gibi, büyük bir olasılıkla Anadolu'da Oligosenden beri bilinen Cricetidae ailesinden Erken Miyosen veya öncesinde türediğini kanıtlar. Kısa sürede Anadolu çevresindeki bölgelere de ulaşan bu ailenin azami dağılımı Kuvaterner'de gerçekleşir. Köstebeklerin salt yeraltı yaşamına uyuşları büyük olasılıkla Geç Miyosen döneminde açık ortamların Batı Asya ve Güneydoğu Avrupa'da yaygınlaşmasına bağlanabilir.

Anahtar Kelimeler: *Biyostratigrafi, evrim, kladistik analiz, Miyosen, Rodentia, Spalacidae, Türkiye.*

INTRODUCTION

The mole rats of the family Spalacidae are burrowing muroid rodents adapted to subterranean life. They have a present day dispersal extending, in the east-west direction, from western Iran to Croatia and, in the north-south direction, from Ukraine to northeastern Africa (Topachevski, 1969). The Anatolian peninsula is situated almost central in their present distribution territory. The fossil localities of the family are also situated within its present dispersal area. The earliest representatives of spalacids are known from Turkey with *Debruijnia arpati* Ünay, 1996, which first occurs at the locality Keseköy in the Neogene Mammalian (MN) Zone 3, and from Greece with *Heramys eviensis* Klein Hofmeijer and de Bruijn, 1985, which first occurs at Aliveri correlated to MN4 (de Bruijn et al., 1992). In the latest Late Miocene, the spalacids appear in the northern Balkans, and much later in Israel and NE Africa (Topachevski, 1969; de Bruijn, 1984; Tchernov, 1986; Popov, 2004). The available fossil record seems to suggest that the spalacids originated in the Middle East, and more probably in Anatolia. Although *Debruijnia* clearly has a cricetid-type dentition, the fossil record does not allow, for the time being, to root this family in a particular genus or species of Cricetidae (Ünay, 1999; Sarıca and Şen, 2003).

The Miocene and Pliocene fossil record of spalacids is quite rich in Turkey, Greece and, to some extent, in SE Europe, but sparse in other territories where the family lives today. In Turkey, more than a dozen Miocene and Pliocene localities have yielded spalacid remains referred to four genera and to eight named species up today. In Greece, they are known with three genera in several Miocene and Pliocene localities. The fossil record is limited, or even absent elsewhere.

As mentioned above, the oldest representatives of this family are included in the genera *Debruijnia* and *Heramys* from the Early Miocene. The genus *Sinapospalax* appeared in the early Middle Miocene and became extinct at the end of the Vallesian (Sarica & Sen, 2003). *Pliospalax* is known from the second part of the Late Miocene (Turolian) and the Pliocene in the Balkans and Turkey. The genus *Spalax* (including *Nannospalax*, see below) appeared in the Late Pliocene (Topachevski, 1969; de Bruijn, 1984). It has to be mentioned here that the genus *Prospalax* Mehely, 1908, known from a few Late Miocene – Early Pliocene localities in central and southeastern Europe, belongs in fact to the family Anomalomyidae (Bolliger, 1999).

Thanks to their relatively rich record in the Balkans and Anatolia, and also to their evolutionary dynamics, spalacids are a useful biostratigraphic tool for terrestrial Neogene deposits (Ünay, 1999; Nesin and Nadachowski, 2001; Sarıca and Şen, 2003). In addition, their subterranean adaptation is interpreted in terms of climatic changes, which occurred in western Asia and southeastern Europe during the Late Miocene (Ünay, 1999; Flynn, 2009).

The aims of the present paper are firstly the description of new spalacid fossils from three Middle and Late Miocene localities of southwestern Anatolia, and, secondly, the discussion of the systematics of the family Spalacidae with the aid of a thorough review of fossil species and of a cladistic analysis of their dental morphology which clears up phylogenetic relationships between species. The names of the genera and species discussed in this paper, as well as the localities where they have been found are given in Appendix 1.

The new material described in this paper is still under study in the Paleontology Laboratory

of the Natural History Museum in Paris. After its study, it will be stored at the Natural History Museum of Ankara. The dental terminology used in this paper is after Sarıca and Şen (2003). The maximum length and width of each tooth were measured using a double axis Mitutoyo measuroscope and are given in millimeters. The upper molars are abbreviated as M1, M2, M3 and lower molars as m1, m2, m3. For ease of comparison, all specimens were illustrated as left; if the original is a right tooth, its number on the figure is underlined.

SYSTEMATICS OF SPALACIDAE

The status of spalacids as a family or subfamily and their relationships with other rodent families have been debated since more than a century (see Ünay, 1999, and references therein). Cranial, postcranial, dental and genetic features of spalacids show that they are closely related to Muroidea, among which they form a separate subfamily (McKenna and Bell, 1997) or a family, the Spalacidae Gray, 1821 (Musser and Carleton, 2005). According to Musser and Carleton (2005: 907), this family contains all extant "species of fossorial and subterraneous muroids arranged in the Myospalacinae (zokors, *Eospalax* and *Myospalax*), Rhizomyinae (bamboo rats *Cannomys* and *Rhizomys*), Spalacinae (blind mole rats, *Spalax*), and Tachyoryctinae (African mole rats, *Tachyoryctes*)".

Such a classification implies that these four subfamilies form a monophyletic group, derived from a common ancestor. Fossil data contradict or at least do not confirm this assumption. Bendukidze et al. (2009: 353) rightly noted that this is not at all the case: "Our reasons to consider Rhizomyinae, Spalacinae, Anomalomyinae and Tachyoryctinae to be separate subfamilies are that the oldest representative of each of these groups: *Prokanisamys arifi* de Bruijn et al., 1981, *Debruijnia arpati* Ünay, 1996, *Anomalomys aliveriensis* Klein Hofmeijer and de Bruijn, 1985 and *Tachyoryctoides obrutschevi* Bohlin, 1937 differ more from each other than some of the later representatives of these groups do. Other evidence for this interpretation comes from the stratigraphical and geographical ranges

of these subfamilies. The early history of the Rhizomyinae seems to have taken place on the Indian subcontinent during the Miocene (Flynn, 1982), that of the Spalacinae in the Middle East during the Miocene (Ünay, 1996), that of the Anomalomyinae in Central Europe during the Miocene (Bolliger, 1999) and that of the Tachyoryctoidinae in Central Asia during the Oligo/Miocene". The great morphological differences of the oldest representatives of these taxa and their apparently different evolutionary history led most paleontologists to consider these groups as separate families, issued independently from early Muroidea sometime in Late Oligocene-Early Miocene. In other words, the fossorial and subterraneous adaptations in these groups resulted in the appearance of similar morphological features, which indicate an evolutionary convergence rather than a descent from a common ancestor. It is also this opinion that we share, since we consider that the fossil and extant blind mole rats belong to an independent family, the Spalacidae.

As noted above, the oldest record of this family is *Debruijnia arpati* Ünay, 1996 from the Early Miocene (MN 3 zone) of Keseköy in Turkey. Several other Early Miocene localities in Turkey also yielded *Debruijnia arpati* or *Debruijnia* sp. (Sabuncubeli, Söke, Dededağ, Gördes-Kınık 1, Kalecik-Sülüklügöl: Ünay, 1996; Ünay and Göktaş, 1999, 2000; de Bruijn et al. 2006, and unpublished data). The other fossil genera included in the Spalacidae are *Heramys* from Greece and Turkey (MN4-MN10), *Sinapospalax* from Turkey (MN5-MN10) and *Pliospalax* from Eastern Europe, Balkan Peninsula and Turkey (MN12-MN16) (references in Sarıca and Şen, 2003).

The systematics of extant species of Spalacidae is also a matter of debate. Zoologists generally agree that there are more than 13 species that Musser and Carleton (2005) found recognizable. However, these authors mention their agreement with Nevo et al. (1995: 226) who noted that "40-50 karyotypes described in Spalacidae represent presumptive good biological sibling species" and that "the morphological species concept does not hold in *Spalax*". Musser and Carleton (2005) grouped all extant species in the genus *Spalax* waiting for extensive studies

integrating morphology (external and anatomic characters), karyotypes and biochemical data within the framework of a cladistic analysis. We have, however, to note that some authors (Topachevski, 1969; de Bruijn, 1984) distinguished two genera: *Nannospalax* Palmer, 1803 (= *Microspalax* Mehely, 1909, its junior synonym) and *Spalax* Guldenstaedt, 1770. It is out of the scope of this paper to enlarge the debate on the generic status of extant species.

The classification of fossil spalacids is mostly based on the morphology of cheek teeth and to some extent of the mandible. The family Spalacidae has been recognized as a monophyletic taxon (Ünay, 1996, 1999; Sarıca and Şen, 2003). Up today, four fossil genera are included in the family Spalacidae: *Debruijnia*, *Heramys*, *Sinapospalax*, *Pliospalax*, in addition to the subfossil and extant genus *Spalax*. At present, the genus *Debruijnia* is known with one species; there are two species referred to *Heramys*, six species to *Sinapospalax* and five other to *Pliospalax*. The only fossil species referred to *Spalax* is *S. odessanus* known from the Late Pliocene (MN 15) localities of the Odessa Catacombes (Ukraine) and Megalo Emvolon (Greece) (Topachevski, 1969; de Bruijn, 1984).

LOCALITIES AND THEIR FAUNAS

Three localities in southwestern Anatolia have yielded new spalacid material, which is described in this paper. These localities are Berdik-1, Direcik-1 and Amasya (Fig. 1). Western Anatolia is shaped by a number of grabens and horsts due to the extensional tectonics that has been active in this region since at least the Early Miocene. There are two types of grabens. The major grabens, such as Büyük Menderes, Küçük Menderes and Gediz-Alaşehir grabens, have an E-W orientation. The second type of grabens, less developed than the previous ones, is generally oriented NE-SW in the north and NW-SE in the south of the Büyük Menderes graben (Fig. 1). All these grabens are bounded by major faults and separated by horst-type reliefs. In a recent review of the local graben structure, Gürer et al. (2009) suggested a two-step model for their creation, the first dealing

with approximately N-S directed grabens which were formed in the Early Miocene under an E-W compressive-transpressive tectonic regime, while the E-W trending major grabens of western Anatolia, such as Büyük Menderes and Gediz-Alaşehir grabens, were formed much later, during the Late Pliocene and Pleistocene, under the effect of the N-S extensive tectonics. The Bozdoğan graben where the Direcik-1 and Amasya localities are situated was formed during the first phase.

The locality of Berdik-1 (Çamoluk, Muğla department) is in the Kale-Tavas Basin, to the south of the Bozdoğan graben (Fig. 1: loc. 1). Its coordinates are N 37° 27' 52.9" and E 28° 35' 49.5". The sedimentary infill of this basin forms two distinct depositional sequences. Late Oligocene-Early Miocene fluvial, lagoonal and shallow marine deposits, developed on the Lycian nappes (Becker-Platen, 1970; Koçyiğit, 1984; Hakyemez, 1989; Yılmaz et al., 2000; Akgün and Sözbilir, 2001; Gürer and Yılmaz, 2002), characterize the lower sequence. The upper sequence is made up of Middle-Late (?) Miocene fluvial and lacustrine deposits, which unconformably overlie the lower sequence (Hakyemez, 1989; Yılmaz et al., 2000). The upper sequence includes irregular intercalation of clayey limestones, limestones, marls, and brownish coal lenses with remnants of small mammals, freshwater gastropods, ostracods and pollen (Sekköy Beds in Becker-Platen, 1970). The Berdik-1 small mammal locality is found in the upper sequence cropping out 1 km west of Çamoluk village (new name of Berdik, Figure 1), in an intermittent up-stream valley to the northern part of Haciosmanbeleni ridge (in the northeastern quarter of the Denizli N 21-a1 topographic sheet). The outcrop is made up of medium- to thick-bedded yellowish limestones and marls including abundant shell fragments and brownish coal seams. This locality has been discovered in the late 1960s by a German team during coal investigations, in collaboration with the Geological Survey of Turkey (MTA). The faunal list given by Sickenberg et al. (1975) and later revised in subsequent studies (Gaziry, 1976; Engesser, 1980; Rummel, 1998) includes *Desmanella* sp., *Desmanodon*
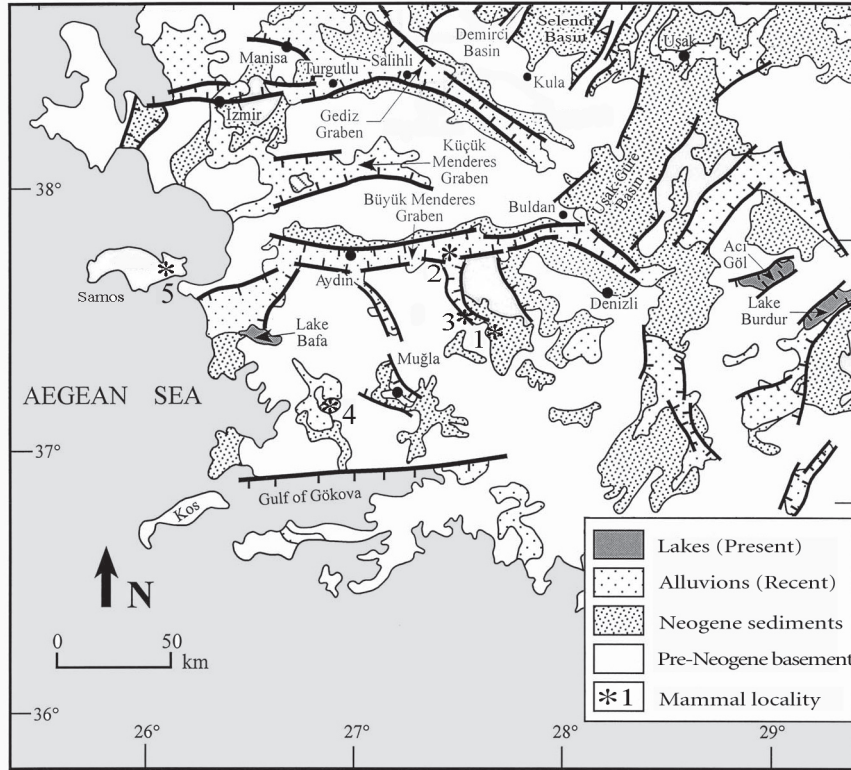
Figure1. Simplified geological map of southwestern Turkey showing Neogene and Quaternary basins (modified from Bozkurt, 2003). The mammal localities with spalacids discussed in this paper are (1) Berdik-1, (2) Direcik-1, (3) Amasya, (4) Sarıçay and (5) Mytilini B in Samos Island.

Şekil 1. Güneybatı Anadolu'nun Neojen ve Kuvaterler havzalarını gösteren basitleştirilmiş haritası (Bozkurt, 2003'den değiştirilerek alınmısıir). Bu yayına konu olan Spalacidae fosillerinin bulunduğu lokaliteler (1) Berdik-1 (2) Direcik-1, (3) Amasya, (4) Sarıçay and (5) Mytilini B (Sisam adası).

cf. *minor*, *Alloptox* cf. *gobiensis*, *Keramidomys* sp., *Myomimus* sp., *Cricetodon candirensis*, *Megacricetodon* aff. *similis*, *Democricetodon brevis*, *D. freisingensis* and *Gomphotherium* sp. Our sampling in this locality yielded, in addition to the spalacid described here, the following rodent species: *Cricetodon candirensis, Megacricetodon* aff. *similis, Democricetodon brevis, D. freisingensis, Keramidomys* cf. *catalanicus* and *Eomyops* sp. (Sarıca-Filoreau, 2002). Comparison with similar Middle Miocene faunas (Paşalar, Çandır, Sarıçay, Yeni Eskihisar, etc.) resulted in the localities correlation to MN7 (late Middle Miocene); it is probably younger than the first three localities and older than the latter one (Sarıca-Filoreau, 2002).

The locality of Direcik-1 (Fig. 1, loc. 2) is situated to the north of the Bozdoğan graben, about one kilometer southeast to Direcik village, at the eastern flank of Naldöken Tepe. Its GPS coordinates are N 37° 45' 58.5" and E 28° 17' 34.1". The fossils come from a mudstone horizon included in the lower sedimentary unit of the Bozdoğan graben. This locality yielded only small mammals determined as *Byzantinia* aff. *dardanellensis, Byzantinia* n. sp., *Megacricetodon debruijni*, Cricetidae indet. *Myocricetodon eskihisarensis, Sinapospalax* sp., *Myomimus dehmi, Microdyromys* sp., Gliridae indet. and *Lophocricetus* sp. Based on this fauna, this locality is correlated to early MN9 zone, i.e. early Late Miocene (Sarıca-Filoreau, 2002).

The locality of Amasya (Bozdoğan, Aydın dept.) is situated in the eastern border of the Bozdoğan graben, 1.5 km NW of the town of Amasya (Fig. 1: loc. 3), on the field road along the cliffs overhanging the river Akçay (Sickenberg et al., 1975). The fossiliferous horizon is included in the fluvio-lacustrine deposits, which cover the metamorphic basement with a fault contact. The fossils

are included in a thin layer of marls below a thick limestone bed. The coordinates of the locality are N 37° 39' 05.2" and E 28° 28' 49.6". This locality yielded both small and large mammals including the hyaenid *Adcrocuta eximia* (Schmidt-Kittler, 1976), the proboscidean *Tetralophodon grandincisivus* (Gaziry, 1976), some ruminants (Sickenberg et al., 1975), the perissodactyles *Hipparion* sp., *Chilotherium schlosseri* and *Ceretotherium neumayri* (Sickenberg et al., 1975; Staesche and Sondaar, 1979), the insectivores *Schizogalerix* n. sp., *Desmanella amasyae, Amblycoptus* sp. and Soricidae indet. (Engesser, 1980) and nine species of rodents: *Parapodemus gaudryi, Apodemus gudrunae, Hansdebruijnia neutrum,* Muridae n. gen. n. sp., *Byzantinia uenayae, Hypsocricetus strimonis,* Cricetidae indet., *Pseudomeriones* sp. and a spalacid (Rummel, 1998; Sarıca-Filoreau, 2002). It is correlated to MN13, i.e. latest Late Miocene (Sarıca-Filoreau, 2002).

In the following pages the spalacids from these three localities are described.

SYSTEMATIC STUDY

Family SPALACIDAE Gray, 1821

Genus *SINAPOSPALAX* Sarıca and Şen, 2003

Type species *Sinapospalax canakkalensis* (Ünay, 1981)

Sinapospalax berdikensis n. sp.

Holotype: isolated left M1, B-7001, (Fig. 2a-b), length x width = 2.84 x 2.33

Hypodigme: nine isolated molars: two M2, two M3, two m1, one m2, two m3.

Type locality: Berdik-1 (Çamoluk, Muğla department).

Derivato nominis: derived from the name of Berdik village.

Measurements: Table 1.

Diagnosis - Medium sized *Sinapospalax* species. Molars longer than wide, with deep and narrow re-entrant folds. Lower molars with transverse sinusid, upper molars with anteriorly directed hook-shaped sinus. Upper molars with segmented endoloph. M1 with transverse

protolophule and metalophule, strong posteroloph and crescent-shaped hypocone. M2-3 with five transverse lophs and four labial re-entrant folds. M2 occlusal outline strongly rounded. M3 with open sinus and cusp-shaped paracone. m1 with ovoid outline; arc-shaped anteroconid firmly connected to metaconid; longitudinal posterior metalophulid connected to posterior arm of protoconid. m2 with a short lingual anterolophid and a transverse hypolophulid. m3 with posteriorly directed hypolophulid and transverse posterolophid.

Differential diagnosis - *Sinapospalax berdikensis* n. sp. differs from all the other species of *Sinapospalax* in having relatively elongated m2, m3 and M3, m2 with confluent hypolophulid and hypoconid, m3 with anteriorly oblique entoconid. It differs from *S. primitivus* in having a metaconid not completely included into the anterolophid and deeper protosinusid in m1, and an open posterosinus in M2. *S. berdikensis* differs from *S. marmarensis* in having higher crowned molars, from *S. canakkalensis, S. incliniformis* and *S. sinapensis* in having a well-rounded anterior outline of m1, with anteroconid completely included in anterolophid, M2 with rounded posterior outline and m2 with rounded antero-labial corner instead of a sharp one. It differs from all species included in the genus *Pliospalax* in having M1 with transverse protolophule and metalophule, M2 and M3 with five transverse lophs and four labial sinuses. It differs from *Heramys* and *Debruijnia* in having larger and higher-crowned cheek teeth.

Description

The cheek teeth of Spalacidae from Berdik-1 are represented by a pair of left and right m1, m3, M2 and M3. The great similarity in size and morphology of the molar pairs, as well as their similar wear stages, indicate that they apparently belong to the same individual (Figures 2 and 3).

M1 (Fig. 2a-a') - The M1 is longer than wide. The anterocone, paracone, metacone and posteroloph are separated from each other by deep labial valleys. The anterocone and protocone are fused to form a curved anterior loph.

Table 1.   Material and measurements (in millimetres) of Sinapospalax berdikensis n. sp. from Berdik-1; l = left, r = right.

Tablo 1.   Berdik-1 lokalitesinde bulunan Sinapospalax berdikensis n. sp. dişlerinin uzunluk ve genişlik ölçüleri.

Specimen number	Molar	Length	Width
B-7001 (Holotype)	M1 (l)	2.84	2.33
B-7002	M2 (l)	2.41	2.19
B-7003	M2 (r)	2.40	2.17
B-7004	M3 (r)	1.93	1.79
B-7005	M3 (r)	1.95	1.79
B-7006	m1 (l)	2.69	2.03
B-7007	m1 (r)	-	-
B-7008	m2 (l)	2.77	2.35
B-7009	m3 (l)	2.53	-
B-7010	m3 (r)	2.50	1.99

The protolophule is connected to the endoloph just behind the protocone. The endoloph is longitudinal and fragmented. The mesoloph is short and posteriorly directed. The metalophule is almost transversal, and joins the posterior arm of the hypocone. The hypocone is crescent-shaped. The posteroloph is directed backwards. It ends free before reaching the labial border. The sinus is directed forwards, and penetrates the occlusal surface. The roots are not preserved.

M2 (Fig. 2b-b', c-c') - The M2 is longer than wide and has a rather rounded outline. The posterior part is slightly narrower than the anterior part. The labial branch of the anteroloph is long and may be connected to the paracone or separated by a notch. The lingual branch is absent. The protolophule is almost transverse and connected to the anterior part of the protocone. The protocone and hypocone are crescent-shaped. They are weakly connected via a fragmented endoloph. The mesoloph is short and wedges-out in the mesosinus without joining the mesostyle; it divides the mesosinus into two valleys. The paracone has anterior and posterior spurs. The sinus is hook-shaped and anteriorly directed. It is deep as the homologous one in the M1. The metalophule is confluent with the posteriorly oriented metacone. It joins the posteroloph just behind the hypocone.

The posteroloph is short and separated from the metacone by a shallow posterosinus.

M3 (Fig. 2d-d', e-e') - The M3 has a subtriangular outline and is longer than wide. It presents a complete occlusal pattern with five transverse lophs. The anterior part resembles that of the M2. The posterior part is reduced. The paracone, mesoloph and metalophule are separated by shallow valleys on the labial side. The metacone is completely included into the transverse metalophule. The posterosinus is enclosed. The endoloph is fragmented. The protocone and hypocone are closely situated.

m1 (Fig. 3a-a', b-b') - Its occlusal outline is rather elongated. The anterior part of the occlusal surface is rounded. It consists of an arc-shaped loph including anteroconid, anterolophid and metaconid, which still has a cusp appearance. The anterolophulid is spur-like, attached on the posterior wall of the anteroloph and not connected to the protoconid. The posterior metalophulid is almost longitudinal. The posterior arm of the protoconid is distinct and joins the posterior metalophulid. The mesolophid is long and wedges out close to the labial border next to the entoconid. The sinusid is transverse and penetrates deeply the occlusal surface, reaching more or less the crown base. The protosinusid is deep as half of the sinusid on the labial side. The mesosinusid is deep on the lingual
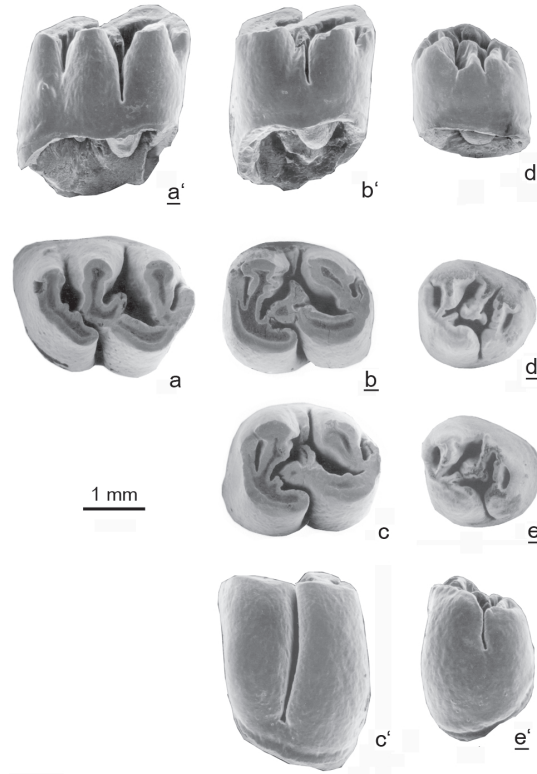
Figure2. Upper molars of Sinapospalax berdikensis n. sp. from Berdik-1. a-a': M1 in occlusal and labial views (B-7001, holotype); b-b': M2 in occlusal and labial views (B-7003); c-c': M2 in occlusal and lingual views (B-7002); d-d': M3 in occlusal and labial views (B-7005); e-e': M3 in occlusal and lingual views (B-7004). In this and following figures, all specimens are shown as left; the underlined specimens are right and have been horizontally flipped.

Şekil 2. *Berdik-1'de bulunmuş Sinapospalax berdikensis n. sp.'nin üst azı dişleri. a-a': M1'in yüzey ve dıştan görünümü (B-7001, holotip); b-b': M2'nin yüzey ve dıştan görünümü (B-7003); c-c': M2'nin yüzey ve içten görünümü (B-7002); d-d': M3'ün yüzey ve dıştan görünümü (B-7005); e-e': M3'ün yüzey ve içten görünümü (B-7004). Bu ve bunu izleyen şekillerde bütün dişler sol olarak gösterildi. Sağ yana ait olan dişler yatay olarak döndörüldü.*

side. The posterolophid is strong and ends free at the lingual side. The roots are not preserved.

m2 (Fig. 3c-c') - The m2 is longer than wide. The anterolophid is reduced and arc-shaped. It defines the inflated anterolabial outline of the m2. The lingual branch of the anterolophid is short, while the labial branch joins the protoconid transforming the protosinusid into a quite large enamel island. The metalophulid is directed forwards. The mesolophid is long and divides the mesosinusid into two valleys. The hypolophulid is incomplete and confluent with the anterior arm of the hypoconid. Therefore, the hypolophulid, hypoconid and posterolophid form a continuous U-shaped lophid. The posterolophid is separated from the entoconid by a relatively shallow posterosinusid. The sinusid is transverse and

deep as the homologous one in the m1. The depth of the mesosinusid is also comparable to that of the m1. The roots are not preserved.

m3 (Fig. 3d-d', e-e') - The m3 is longer than wide, and has a sub-triangular outline with a reduced posterior part. The lingual anterolophid is weak. It joins the metaconid enclosing the anterosinusid as an enamel island. The labial anterolophid is absent. The metalophulid is curved forwards to join the anterolophid in front of the protoconid. The protoconid and anterolophid are separated by a notch on the antero-labial border, which is interpreted as a relic protosinusid. A short mesolophid is present. The hypolophulid is directed backwards. The posterolophid is weak, transverse and separated from the hypolophulid by a
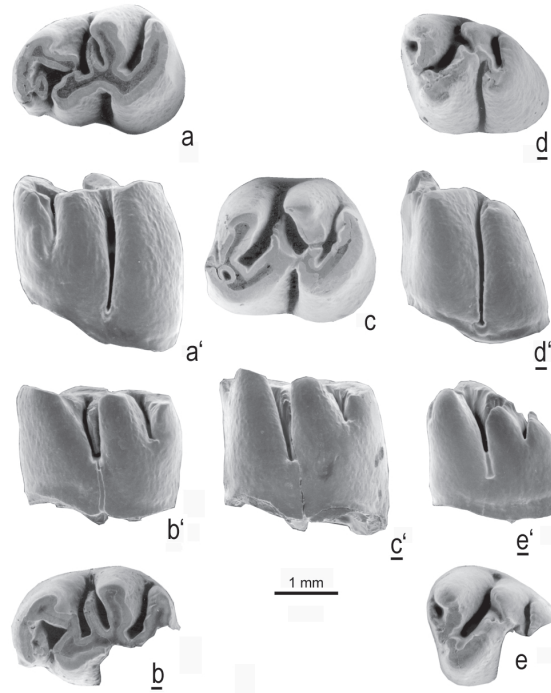
Figure 3. Lower molars of Sinaspospalax berdikensis n. sp. from Berdik-1. a-a': m1 in occlusal and labial views (B-7006); b-b': m1 in occlusal and lingual views (B-7007); c-c': m2 in occlusal and lingual views (B-7008); d-d': m3 in occlusal and labial views (B-7010); e-e': m3 in occlusal and lingual views (B-7009).

Şekil 3. Berdik-1'de bulunmuş Sinaspospalax berdikensis n. sp.'nin alt azı disleri. a-a': m11'in yüzey ve dıştan görünümü (B-7006); b-b': m11'in yüzey ve içten görünümü (B-7007); c-c': m2'nin yüzey ve içten görünümü (B-7008); d-d': m3'ün yüzey ve dıştan görünümü (B-7010); e-e': m3'ün yüzey ve içten görünümü (B-7009).

notch. The sinusid is transverse and deep as in the preceding molars.

Comparison

The elongated form of the m2, m3 and M3 and the complete dental pattern of the M3 from Berdik-1 remind the dental features of *Debruijnia*, and are interpreted as primitive. However, the teeth from Berdik-1 are considerably larger in size (Fig. 4), and have derived features shared with *Sinaspospalax* such as higher crowned and more lophodont cheek teeth with thicker ridges and deep and narrow sinus(id)s (Figs. 5-9). The other apomorphic characters of the spalacid from Berdik-1 are the curved and short anterolophid, incomplete hypolophulid confluent with the hypoconid in m2, and posteriorly directed hypolophulid in m3 (Fig. 3).

Among the species of *Sinaspospalax, S. primitivus* (Ünay 1978) is the species having greater similarity with the spalacid from Berdik-1 than the others. The molars from Berdik-1 are in the lower size limit of *Sinaspospalax primitivus,* in particular for the M2, M3 and m1 (Fig. 4: Saricay). This species and Berdik-1 specimens share several characters: M2 with a rounded outline and an anteriorly connected protolophule (Fig. 6), m1 with a rounded and arc-shaped anterolophid, and transverse sinusid (Fig. 7). However, the presence of a distinct metaconid and a deeper protosinusid in the m1 (Fig. 7), transverse protolophule and metalophule in the M1 and an open posterosinus in the M2 (Fig. 6) from Berdik-1 distinguishes the new material from *S. primitivus*. The presence of an open posterosinus in the M2 and a metaconid not completely included into the anterolophid in the m1 of *S. berdikensis* n. sp. suggest that it should be older than *S. primitivus*.

Sinaspospalax marmarensis is the smallest species of this genus (Fig. 4: Pasalar (P)). Its molars show some primitive features such as low crown height (Fig. 8), thinner lophs, squarish
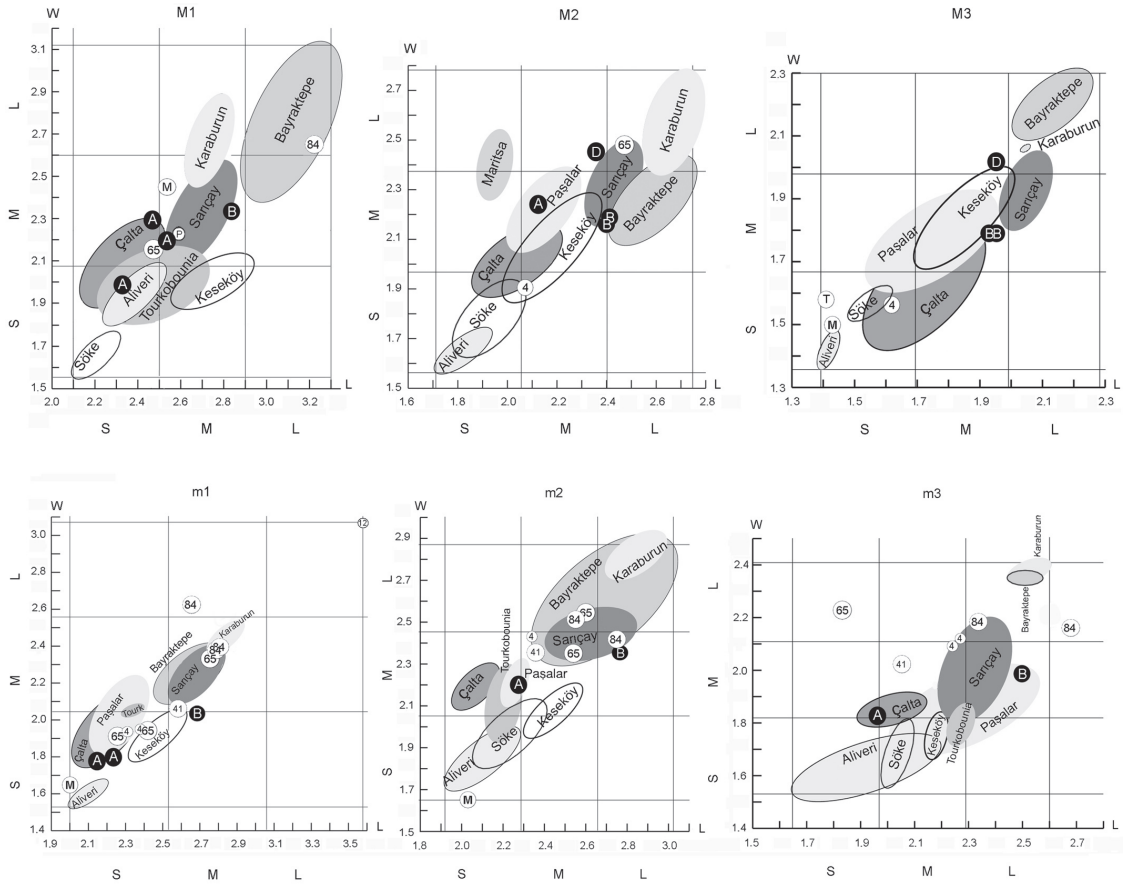
Figure 4. Length-width scatter diagrams of upper and lower molars of Spalacidae from different localities. Legend for L/W scatter diagrams: Berdik-1 (B): Sinapospalax berdikensis n. sp., Direcik-1 (D): Sinapospalax sp., Amasya (A): Pliospalax complicatus n. sp., Aliveri: Heramys eviensis; Bayraktepe: Sinapospalax canakkalensis; Çalta: Pliospalax macovei; Karaburun: Spalax odessanus; Keseköy: Debruijnia arpati; Maritsa (M): Pliospalax sotirisi; Paşalar (P): Sinapospalax marmarensis; Sarıçay: Sinapospalax primitivus; Tourkobounia (T): Pliospalax tourkobouniensis. Numbers refer to Sinap Formation localities: 4: Heramys anatolicus; 41: S. incliniformis; 65: S. canakkalensis; 84: S. sinapensis. Size ranges: S: small, M: medium, L: large. (Modified after Sarıca and Şen 2003).

Şekil 4.   Çeşitli Spalacidae türlerinin üst ve alt azı dişlerinin uzunluk/genişlik çizelgesi. Berdik-1 (B): Sinapospalax berdikensis n. sp., Direcik-1 (D): Sinapospalax sp., Amasya (A): Pliospalax complicatus n. sp., Aliveri: Heramys eviensis; Bayraktepe: Sinapospalax canakkalensis; Çalta: Pliospalax macovei; Karaburun: Spalax odessanus; Keseköy: Debruijnia arpati; Maritsa (M): Pliospalax sotirisi; Paşalar (P): Sinapospalax marmarensis; Sarıçay: Sinapospalax primitivus; Tourkobounia (T): Pliospalax tourkobouniensis. Sinap formasyonu lokalitelerinin numaraları 4: Heramys anatolicus; 41: S. İncliniformis; 65: S. canakkalensis; 84: S. Sinapensis. Boyut değerleri: S: küçük, M: orta, L: büyük. (Sarıca ve Şen, 2003'den değiştirilerek alınmıştır).

outline of M2 (Fig. 6) and m2 (Fig. 9), distinct anteroconid and metaconid on m1 (Fig. 7) (more or less fused in other species), and strong lingual anterolophid on m2 and m3 (Fig. 9). These characters are not observed on the Berdik-1 specimens.

Sinapospalax canakkalensis is another species which shares several features with the

Berdik-1 material, such as the strong mesolophs and mesolophids on all molars, the almost transverse protoloph and metaloph and hook-shaped sinus on the M1 (Fig. 5), the M3 longer than wide and having protocone and hypocone separated by a deep sinus (Fig. 4). However, *S. canakkalensis* lacks the posterior metalophulid on the m1, the lower molars have a deep sinus posteriorly directed (Figs. 7-8), the metacone

of the M1 is isolated or tends to be isolated, and on the M2 the protolophule is strongly connected to the labial anteroloph (Figs. 5-6).

S. incliniformis from Sinap Loc. 41 (Late Vallesian) is known only with its lower molar. Althoug similar in size, this species differs from that of Berdik-1 in having strongly oblique lophids.

S. sinapensis from the Early Vallesian of Sinap Loc. 84 is larger in size than the specimens from Berdik-1 (Fig. 4). Its molars has lophs thicker, and its lower molars have sinusids deeper than on the specimens from Berdik-1.

Based on its differences in size and morphology from the other species, the Berdik-1 material

is described as a new species of the genus *Sinapospalax*.

Sinapospalax sp.

Locality: Direcik-1 (Nazilli, Aydın department)

Material and measurements: Right M2 (DI-1990: 2.45 x 2.35) and left M3 (DI-1991: 2.04 x 1.95).

Description and comparison

Both teeth are heavily worn. On the M2 (Fig. 10a), the sinus is directed anteriorly; on the lingual crown side it nearly reaches the base of the crown. The anterior mesosinus is still open labially while the posterior one is an oblique enamel island. This pattern suggests that

Figure 5. Morphology of the M1 in Sinapospalax berdikensis n. sp. and Pliospalax complicatus n. sp. compared to some species of Sinapospalax and Pliospalax. I– occurrence of protolophule and metalophule: a) both are transverse, b) protolophule slightly directed backwards and metalophule transverse, c) both directed backwards. II- shape of hypocone: a) crescent-shaped, b) angular. 1 from Ünay, 1981: pl. I-1a; 2 from Ünay, 1990: pl. III-1; 3 from Sarıca and Şen, 2003: fig. 11E; 4 from Şen, 1977: pl. XIII-8. Figures of molars are not to scale (sizes of all M1s are same to facilitate morphological comparison); they are illustrated as left.

Şekil 5. *Sinapospalax berdikensis n. sp. ve Pliospalax complicatus n. sp. M1 yapısının diğer Sinapospalax ve Pliospalax türleriyle karşılaştırılması. I- protoloful ve metaloful yönü: a) enlemesine, b) protoloful hafifce öne dönük, metaloful ise enlemesine, ç) ikisi de arkaya dönük. II- hipokon yapısı: a) ay şeklinde, b) açılı. Kaynaklar: 1: Ünay, 1981: pl. I-1a; 2: Ünay, 1990: pl. III-1; 3: Sarıca and Şen, 2003: fig. 11E; 4: Şen, 1977: pl. XIII-8. Şekiller ölçeğe uyulmadan çizildi ve bütün dişler sol çeneye ait gibi gösterildi.*

Figure 6. Morphology of the M2 in Sinapospalax berdikensis n. sp. compared to some species of Sinapospalax and Pliospalax. I- occurrence of labial lophs and re-entrant folds: a) complete pattern with five lophs and four open re-entrant folds, b) complete pattern with five lophs and enclosed antero- and posterosinus, c) simplified pattern with three lophs and two re-entrant folds. II- outline of M2: a) rounded, b) square. References for data: 1: Ünay, 1981: pl. III-2a; pl. I-5; 2: Ünay, 1990: pl. III-2; 3: Sarıca and Şen, 2003: fig. 11F; 4: Şen, 1977: pl. XIII-5, from the tooth row. Figures of molars are not to scale, and illustrated as if they are from the left side.

Şekil 6.   Sinapospalax berdikensis n. sp. ve Pliospalax complicatus n. sp. M2 yapısının diğer Sinapospalax ve Pliospalax türleriyle karşılaştırılması. I- enlemesine mine sırtları (lof) ve dış girişli vadiler (sinus): a) beş sırt ve dört vadili diş yapısı, b) beş sırt ve dört vadili diş yapısı, fakat ön ve arka vadiler dış yüze kapalı, c) üç sırtlı ve iki vadili basitleşmiş diş yapısı. II- M2'nin şekli: a) yuvarlak, b) kare. Kaynaklar: 1: Ünay, 1981: pl. III-2a; pl. I-5; 2: Ünay, 1990: pl. III-2; 3: Sarıca and Şen, 2003: fig. 11F; 4: Şen, 1977: pl. XIII-5. Şekiller ölçeğe uyulmadan çizildi ve bütün dişler sol çeneye ait gibi gösterildi.

this tooth should have, when unworn, a strong mesoloph situated closer to the paracone than to the metacone. The lingual side of the crown is much higher than the labial one. There are a strong lingual root and two small labial roots.

The M3 (Fig. 10b) has an occlusal outline almost rounded. Because of its heavy wear, all sinuses are reduced to enamel islands. The presence of a groove on the lingual face of the crown suggests that a narrow sinus existed in early stages of attrition. The crown is much higher lingually than labially. The roots are as on the M2, although smaller.

These two upper teeth share the characters of *Sinapospalax* in having moderately high crown, a strong mesoloph and a deep sinus on the M2. Their sizes fit with that of *Sinapospalax*

primitivus, S. canakkalensis and *S. berdikensis*, but it is clearly larger than that of *S. marmarensis*. The limited material from Direcik-1 and its poor state of preservation do not allow further comparison, hence its determination as *Sinapospalax* sp.

Genus *PLIOSPALAX* Kormos, 1932

Type species *Pliospalax macovei* (Simonescu, 1930)

Pliospalax complicatus n. sp.

Holotype: Isolated right m1 A-1096, (Fig. 11d), length x width = 2.23 x 1.80.

Hypodigme: Seven isolated molars: three M1, one M2, one m1, one m2, one m3.
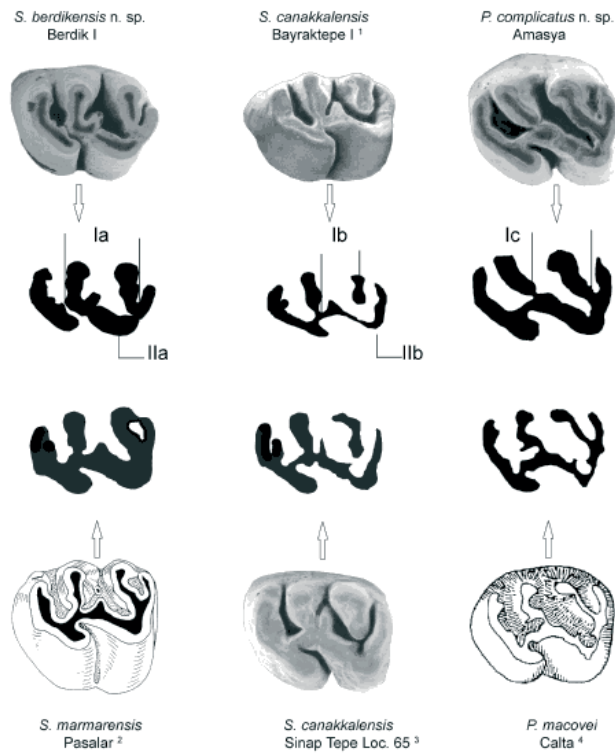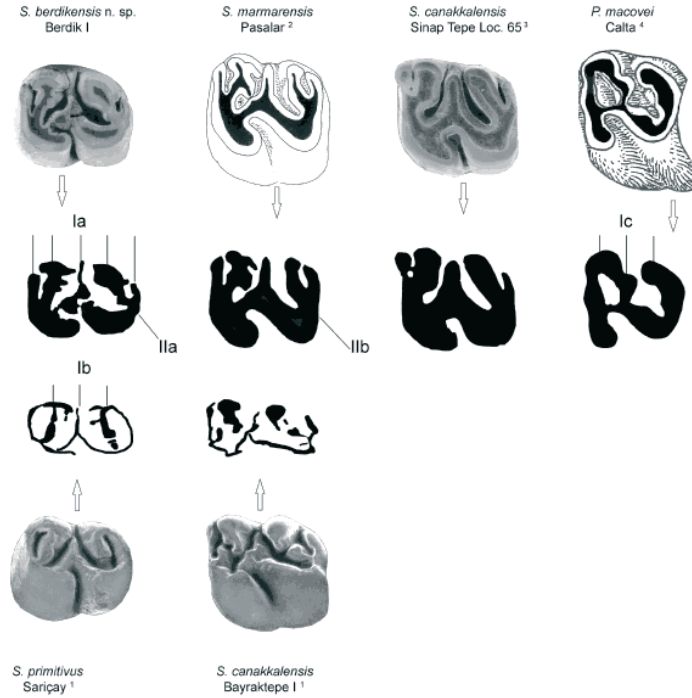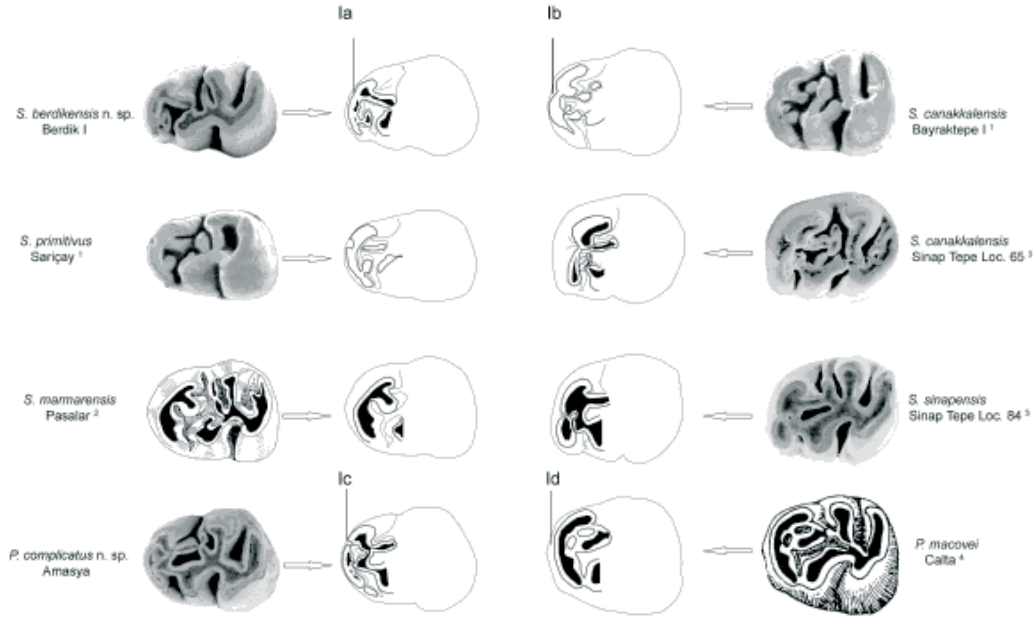
Figure 7. Morphology of m1 in Sinapospalax berdikensis n. sp. and Pliospalax complicatus n. sp. compared to some species of Sinapospalax and Pliospalax. I- occurrence of anteroconid and metaconid: a) anteroconid included into anterolophid and connected to conicle metaconid, b) both are conicle and separated by a notch, c) anteroconid completely included into anterolophid and separated by an anterosinus from conicle metaconid d) both are completely included into anterolophid. References for data: 1: Ünay , 1981: pl. II-2; pl. III-1a; 2: Ünay, 1990: pl. II-1; 3: Sarıca and Şen, 2003: fig. 11B; fig. 14A; 4: Şen, 1977: pl. XIV-3a. Figures of molars are not to scale, and illustrated as if they are from the left side.

Şekil 7. *Sinapospalax berdikensis n. sp. ve Pliospalax complicatus n. sp. m1 yapısının diğer Sinapospalax ve Pliospalax türleriyle karşılaştırılması. I- anterokonid ve metakonid: a) anterokonid anterolofidle kaynaşıktır ve metakonidle bağlantılıdır, b) iki tüberkül de koni şeklinde olup birbirlerinden bir vadiyle ayrılırlar, c) anterokonid anterolofid ile tamamen kaynaşıktır ve koni yapısındaki metakonide bağlı değildir, d) iki tüberkül de anterolofidle kaynaşıktır. Kaynaklar: 1: Ünay , 1981: pl. II-2; pl. III-1a; 2: Ünay, 1990: pl. II-1; 3: Sarıca and Şen, 2003: fig. 11B; fig. 14A; 4: Şen, 1977: pl. XIV-3a. Şekiller ölçeğe uyulmadan çizildi ve bütün dişler sol çeneye ait gibi gösterildi.*

Type locality: Amasya (Bozdoğan, Aydın department)

Derivato nominis: Derived from the complicated pattern of lower first molar.

Measurements: Table 2

Diagnosis**:** Small to medium sized spalacid with high crowned cheek teeth. m1 with anteroconid completely incorporated into an arc-shaped anterolophid, antero-lingually situated conical metaconid, anterosinusid enclosed in early stage of wear, double metalophulid, anteriorly oblique protosinusid, protoconid without a posterior arm, posteriorly directed sinusid. M1 with anteriorly oblique paracone and metacone, without mesoloph.

Differential diagnosis: *Pliospalax complicatus* n. sp. differs from the species of *Heramys*

and *Debruijnia* in having higher crowned, more lophodont cheek teeth. It differs from *Sinapospalax* in having anterosinusid, anteriorly oblique and shallow protosinusid in m1; posteriorly oblique protoloph and metaloph, four transverse lophs and three labial re-entrant folds in M1, and M2. *Pliospalax complicatus* differs from all species of *Pliospalax* and *Spalax* in having a complicated anterior occlusal pattern of m1 with conical metaconid (not included into anterolophid), an anterosinusid, a double metalophulid and in the presence of a long mesolophid in m1-2.

Description

M1 (Fig. 11a)**-** The M1 is longer than wide. There are three labial and one lingual re-entrant folds. The lophs are thick, as large as the cones. The anteroloph is transverse on the anterior border
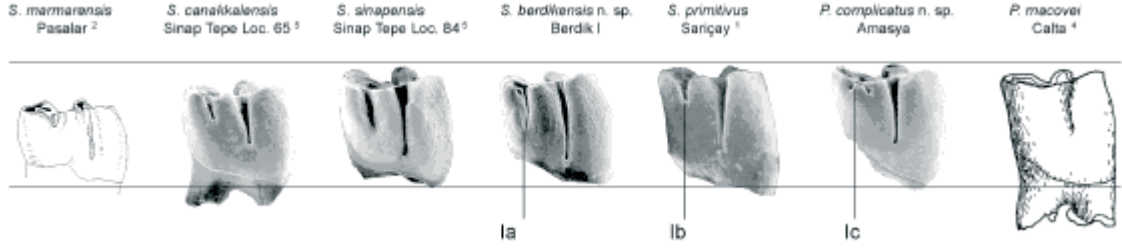
Figure 8. Crown height and occurrence of labial re-entrant folds in m1 of Sinapospalax berdikensis n. sp. and in Pliospalax complicatus n. sp. compared to some species of Sinapospalax and Pliospalax. I- depth of protosinusid: a) deep as half of the sinusid, b) shallower than the half of the sinusid, c) very shallow, disappears by early stages of wear. References for data: 1: Ünay, 1981: pl. III-1; 2: Ünay, 1990: pl. II-1a; 4: Şen, 1977: pl. XIV-3b; 5: labial views of the m1s from Sinap Tepe Loc. 65 and 84 given in Figure 7 from Sarıca and Şen (2003). Figures of molars are not to scale, and illustrated as if they are from the left side.

Şekil 8. *Sinapospalax berdikensis n. sp. ve Pliospalax complicatus n. sp. de m1 taç yüksekliği ve dışa açan vadilerin diğer Sinapospalax ve Pliospalax türleriyle karşılaştırılması. I- protosinusid derinliği: a) sinusidin yarısı kadar veya daha fazla derin, b) sinusidin yarısından daha az derin, c) çok sığ ve aşınma ile çabucak yokolur. Kaynaklar: 1: Ünay, 1981: pl. III-1; 2: Ünay, 1990: pl. II-1a; 4: Şen, 1977: pl. XIV-3b; 5: Sinap Tepe Loc. 65 ve 84 (Sarıca ve Şen, 2003). Şekiller ölçeğe uyulmadan çizildi ve bütün dişler sol çeneye ait gibi gösterildi..*
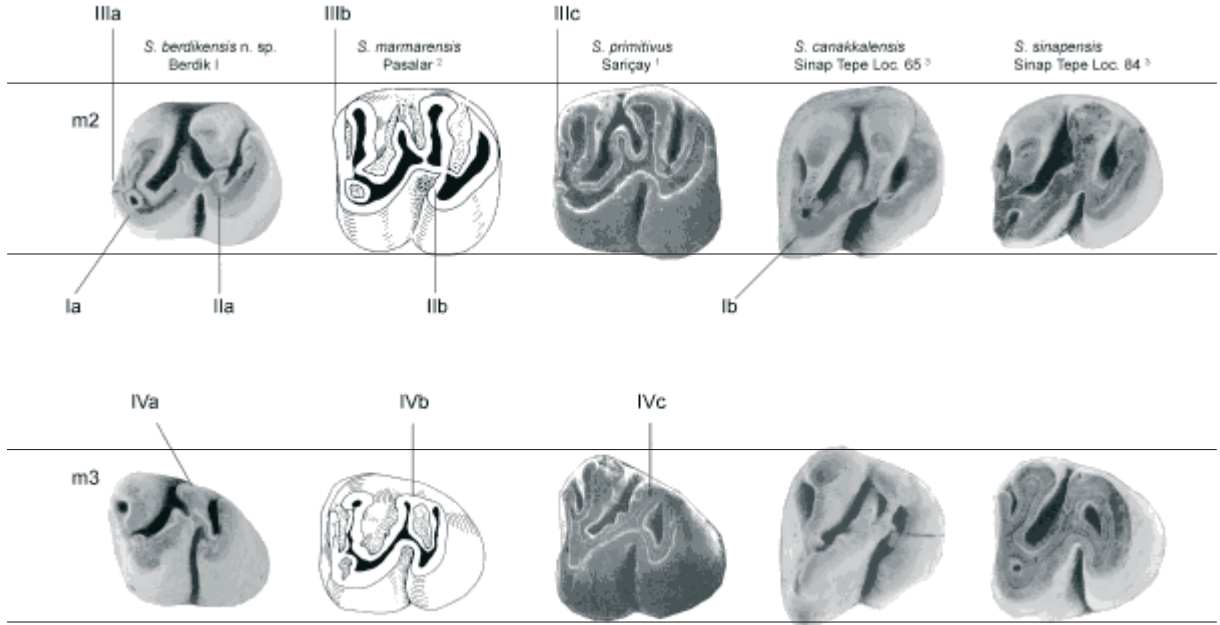
Figure 9. Morphology of m2-3 in Sinapospalax berdikensis n. sp. compared to some species of Sinapospalax. I-shape of anterolabial outline in m2: a) rounded and inflated, b) angular. II- occurrence of hypolophulid in m2: a) confluent with hypoconid, b) separated by a notch from hypoconid. III- occurrence of lingual anterolophid in m2: a) very short, ending on the long axis b) long reaching the lingual border, c) medium length, ending before reaching the lingual border. IV- occurrence of hypolophulid in m3: a) posteriorly directed, b) transverse, c) anteriorly directed. References for data: 1: Ünay, 1981: pl. III-3, 5; 2: Ünay, 1990: pl. II-2, 3; 3: Sarıca and Şen, 2003: fig. 11C, D for Loc 65; fig. 14C, D for Loc. 84. Figures of molars are not to scale, and illustrated as if they are from the left side.

Şekil 9. *Sinapospalax berdikensis n. sp.'de m2 ve m3'ün taç yapısının bazı Sinapospalax türleriyle karşılaştırılması. I- dişlerin ön yüzünün konturu: a) yuvarlak ve şişkin, b) açılı. II- m2'de hipolofulid: a) hipokonid'le kaynaşık, b) hipokonid'den bir vadi ile ayrılmış. III- m3'de iç anterolofid: a) çok kısa , b) uzun ve iç yüz kenarına kadar uzanık, c) orta uzunlukta olup iç kenara kadar ulaşmaz. IV- m3'de hipolofulid: arkaya dönük, b) enlemesine, c) öne dönük. Kaynaklar: 1: Ünay, 1981: pl. III-3, 5; 2: Ünay, 1990: pl. II-2, 3; 3: Sarıca ve Şen, 2003: Loc 65 örneği fig. 11C, D; Loc. 84 örneği fig. 14C, D. Şekiller ölçeğe uyulmadan çizildi ve bütün dişler sol çeneye ait gibi gösterildi.*
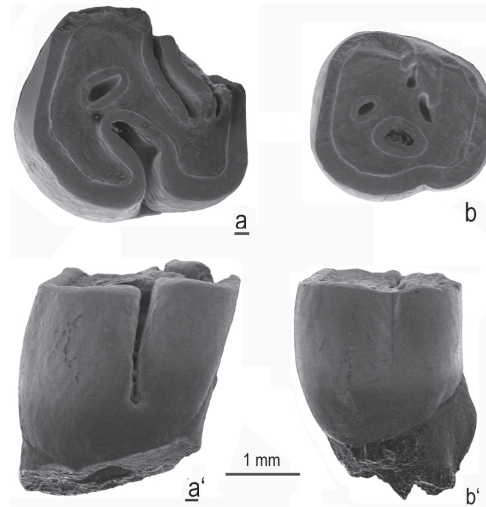
Figure 10. Sinapospalax sp. from Direcik-1. a-a': M2 in occlusal and lingual views (DI-1990); b-b': M3 in occlusal and lingual views (DI-1991).

Şekil 10.   Direcik-1 lokalitesinde bulunmuş Sinapospalax sp. azı dişleri. a-a': M2'nin çiğneme yüzeyi ve iç yüzden görünümü (DI-1990); b-b': M3'ün çiğneme yüzeyi ve iç yüzden görünümü (DI-1991).

and abruptly turns backwards becoming confluent with the protocone. The protoloph and metaloph are parallel to each other and strongly inclined backwards. The paracone is elongated and weakly connected to the endoloph. The metaloph is connected to the posteroloph just behind the hypocone. The mesoloph is absent. The strong posteroloph is lens-shaped and faintly convex. The sinus is anteriorly oblique, and deeply penetrates the occlusal surface. On the labial crown side, the mesosinus is as deep as 1/3 of the crown height, while the anterosinus and the posterosinus are shallow. There are one large lingual and two labial roots.

M2 (Fig. 11b) - The unique M2 is worn. It has a square occlusal outline on which the posterior part is slightly narrower than the anterior part. The sinus and the posterior branch of the mesosinus are still open. The anterior branch of the mesosinus is enclosed as an enamel island. The lamellar form of the dentine area of the M2 allows tracing the occlusal pattern of this specimen attrition. Compared to a *Heramys* M2, which displays a complete dental pattern with five transverse labial lophs, this M2 from Amasya should have four transverse lophs. On the other hand, the paracone and metacone are still cusp-shaped and a trace of a posteroloph is still present, thus the molar has a pattern more complicated than molars of *Pliospalax*

and *Spalax* have. The sinus is shallower than on the M1. There are two labial and one strong lingual roots.

m1 (Fig. 11c and d)- The anterior outline is rounded. The anteroconid is completely incorporated into the anterolophid. The anterolophid is curved from the metaconid towards the labial border of the tooth enclosing the protosinusid. The protosinusid is anteriorly oblique and quite shallow. The metaconid is still cusp-shaped and placed antero-lingually. The metalophulid is double. The anterior metalophulid joins the anterolophid on the long axis together with the anterolophulid. The posterior metalophulid is parallel to the longitudinal axis of the tooth and reaches the mesolophid. The posterior arm of the protoconid is absent. The mesolophid is fragmented; the first fragment is directed forwards and issued from the ectolophid in front of the hypolophulid, joining the posterior metalophulid; the second fragment is transverse and joins the entoconid on the lingual border. The posterolophid is transverse. The sinusid is directed backwards and deep. The roots are not preserved.

m2 (Fig. 11e)- The m2 is worn. The anterior branch of the mesosinusid and the posterosinusid are still open. Because of the attrition, it is not possible to detect whether the

Table 2. Material and measurements (in millimetres) of Pliospalax complicatus n. sp. from Amasya; l = left side, r = right side.

Tablo 2. Amasya lokalitesinde bulunan Pliospalax complicatus n. sp. dişlerinin uzunluk ve genişlik ölçüleri.

Specimen number	Molar	Length	Width
A-1092	M1 (r)	2.47	2.30
A-1093	M1 (r)	2.53	2.20
A-1094	M1 (l)	2.33	1.99
A-1095	M2 (r)	2.13	2.24
A-1096 (Holotype)	m1 (r)	2.23	1.80
A-1097	m1 (r)	2.15	1.78
A-1098	m2 (r)	2.28	2.20
A-1099	m3 (l)	1.96	1.83

anterolophid, protosinusid and anterosinusid are present. Judging on the shape of sinusids and the enamel island, this tooth probably had a metalophulid connected to the base of the lingual anterolophid, and a rather strong mesolophid (Figure 11e'). The posterolophid is curved to join the entoconid on the lingual border. The sinusid is deep as on m1, and directed backwards. There are two roots.

m3 (Fig. 11f) **-** The m3 has a triangular outline with a strongly reduced posterior part. The anterolophid is transverse and defines the straight anterior border of the m3. The metaconid is connected to the anterolophid close to its lingual end, thereby leaving a weak anterosinusid. There is a relic protosinusid between the labial anterolophid and protoconid. The protoconid is still cusp-shaped. The entoconid is reduced. The mesolophid is absent. The mesosinusid is shallow on the lingual view. The hypoconid is strongly reduced and included into the posterolophid. The posterolophid is curved to enclose the posterosinusid. The sinusid is transverse and deep and directed backwards, as in the two preceding molars. The roots are not preserved.

Comparison

The spalacid from Amasya shares some features with *Heramys anatolicus* from Sinap Tepe Loc. 4 (Sarıca and Şen, 2003: Fig. 6.8 A,B) in having an m1 with: 1) an anteroconid incorporated into the anterolophid, 2) a large metaconid

preserving the cusp form, 3) an enclosed anterosinusid, 4) an anterior metalophulid (= central anterolophulid in Sarıca and Şen, 2003), 5) and an anteriorly oblique protosinusid. One can wonder if these characters accord with a direct phylogenetic relation between *H. anatolicus* and *Pliospalax*. However, the Amasya spalacid has higher crowned molars than *Heramys anatolicus* and its M2 is simplified in having three transverse lophs and two labial sinuses. In these respects, this species is more evolved than *Heramys anatolicus*; some resemblances in their dental pattern may have been plesiomorphic features or convergences.

The Amasya spalacid also reminds some species of *Sinapospalax* in having strong mesolophids on m1 (Fig. 7) and m2 (Figs. 9, 11). However, the m1 has a shallow protosinusid (Fig. 7), the protolophule and metalophule are oblique posteriorly in the M1 (Fig. 5), and the M2 pattern is simplified compare to that of *Sinapospalax* species (Figs. 6, 11).

The small-to medium sized Spalacidae cheek teeth from Amasya share the following characters with the species of *Pliospalax*: relatively high-crowned molars with low length/ width ratio, M1 with posteriorly oblique protolophule and metalophule, M2 with three transverse lophs and two labial sinus, m1 with a shallow protosinusid. On the other hand, it differs from all the species of *Pliospalax* in having an m1 with a complicated anterior dental pattern (double

metalophulid, anterosinusid) and stronger mesolophids in m1 and m2. Therefore, the spalacid remains from Amasya are described as a new species of the genus *Pliospalax*.

PHYLOGENY OF SPALACIDAE

As noted above, 16 fossil species and a great number of extant species are grouped in the family of Spalacidae (see Appendix 1 for fossil species). These species are referred to five different genera, four of them being extinct. A generic level cladistic analysis was performed by Sarıca and Şen (2003), which provided a cladogram showing the relationships of these genera as (*Debruijnia* (*Heramys* (*Sinapospalax* (*Pliospalax* (*Spalax*))))). However, it is interesting to test, first of all, the homogeneity of these genera, and the intrageneric relationships among their species. In addition, as noted above, the new species *Pliospalax complicatus* and some other species referred to *Pliospalax* share some dental features with *Heramys* and/or *Sinapospalax*, suggesting some relationships between these genera that the previous cladistic analysis did not revealed. Finally, it is interesting to clear up the phylogenetic relationships among the species referred to these five genera.

Two species were selected as outgroup taxa: *Eucricetodon kurthi* de Bruijn et al. 2003 from the Eocene/Oligocene boundary locality of Süngülü in NE Turkey and *Aralocricetodon schokensis* Bendukidze, 1993 from the Late Oligocene of the Aral Formation in Kazakhstan. The main reason for selecting these species as outgroup taxa is that some authors have already mentioned their dental resemblances. Musser and Carleton (2005: 908) rightly noted that "the dentition of Turkish, African and some Asian forms (fossil Spalacidae *s.l.)* recalls occlusal patterns common to *Eucricetodon*". *Eucricetodon kurthi* is the best known species from the dispersal area of Spalacidae. On the other hand, Bendukidze et al. (2009: 354) marked that "the rather large, robust, semi-hypsodont cheek teeth of *Aralocricetodon* show strong resemblance to those of the Middle Miocene Rhizomyinae from the Indian subcontinent". As discussed above, the Rhizomyinae are considered

to be a sister subfamily of the Spalacinae, sensu Musser and Carleton (2005). Bendukidze (1993) and Lopatin (2004) referred *Aralocricetodon* to Cricetodontinae, but according to Bendukidze et al. (2009) it should be included in the Tachyoryctoidinae. Its dentition shares some apomorphic features with that of the Spalacidae.

The ingroup taxa consist of 16 species referred to the genera *Debruijnia, Heramys, Sinapospalax, Pliospalax* and *Spalax*. As shown in Appendix 1, the samples analyzed for character states are almost all from the type localities of species. If a species is better known from another locality, the new materiel was also included in the character analysis under the name of the species+locality. In addition, the material referred to a species as cf. (for instance *Sinapospalax* cf. *marmarensis* from the Middle Miocene locality of Çandir in Turkey) was also taken in consideration, of course separately.

A cladistic analysis using Mesquite version 2.72 (Maddison and Maddison, 2009) was conducted (Figure 12). 58 phylogenetically informative characters of the upper and lower molars were selected and their character states were identified using the main diagnostic features (Appendix 2). The characters of the skull and mandible, and those of incisors were not analyzed because they are not known in most fossil species. For character analysis, we used our own observations on the original material, when available, or the descriptions and illustrations in the related papers. 42 characters are binary and 16 others have three or more states (Appendix 2). Due to the lack of a priori information, the weight of all characters is identical (1). Because there is no rationale to order the multistate characters, all possible transformations of one state into another will cost one step. The relatively high number of terminal taxa and characters precluded the use of exact algorithms, and so a heuristic search by stepwise addition ('add & rearrange') was performed to obtain 300 trees, of which a Strict Consensus Tree was calculated (Figure 12). The values for the Strict Consensus Tree are: treelength = 212, CI = 0.618 and RI = 0.7.

As shown in Figure 12, the phylogenetic relationships of *Debruijnia arpati, Heramys eviensis*
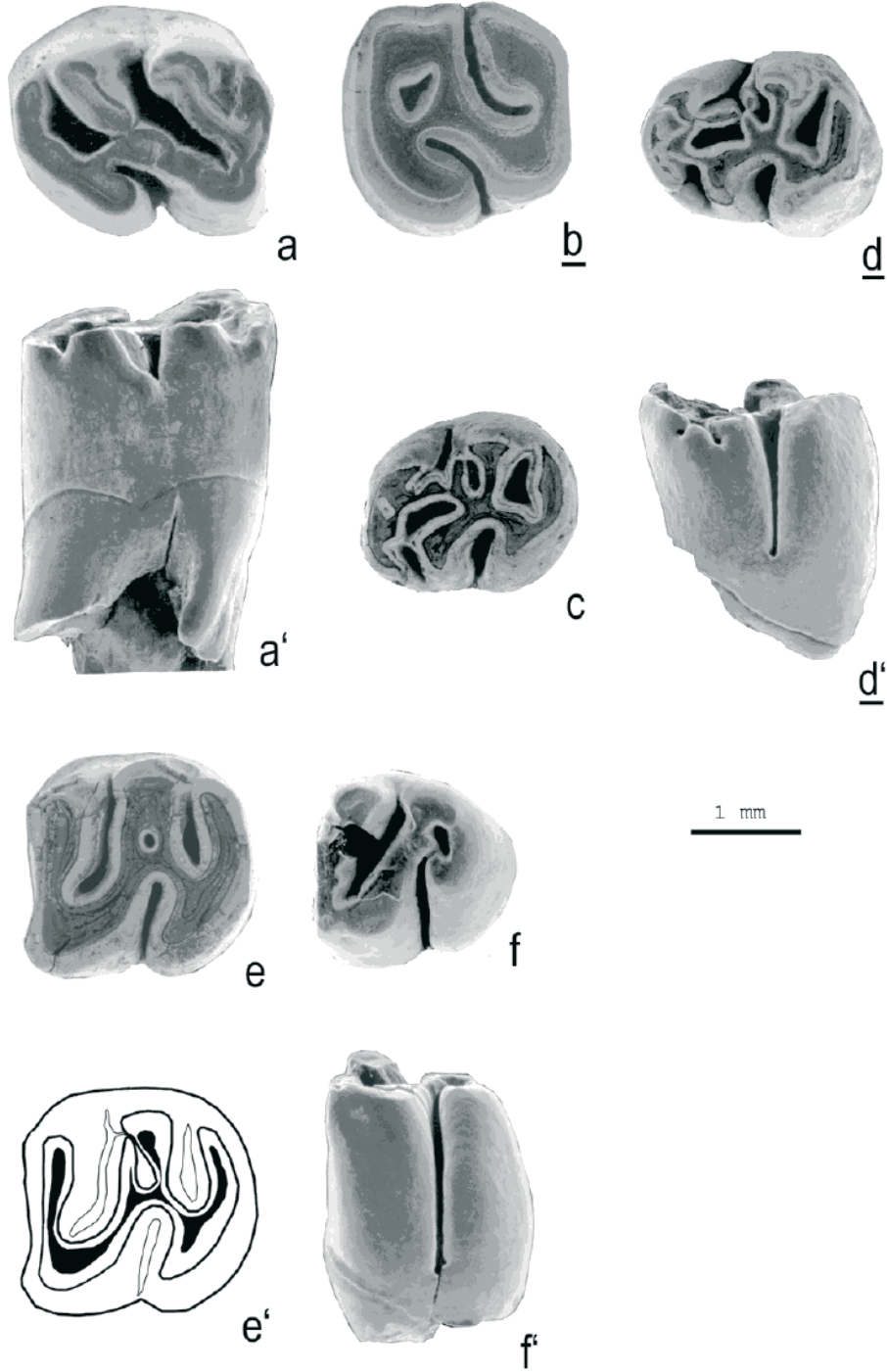
Figure 11. Pliospalax complicatus n. sp. from Amasya. a-a': M1 in occlusal and labial views (A-1092); b: M2 in occlusal view (A-1093); c: m1 in occlusal view (A-1095); d-d': m1 in occlusal and labial views (A-1096, holotype); e-e': m2 in occlusal view and its supposed initial pattern (A-1098) f-f': m3 in occlusal and labial views (A-1099).

Şekil 11. Amasya lokalitesinde bulunmuş Sinapospalax complicatus n. sp. azı dişleri. a-a': M1'in çiğneme yüzeyi ve dış yüzden görünümü (A-1092); b: M2'nin çiğneme yüzeyi görünümü (A-1093); c: m1'in çiğneme yüzeyi görünümü (A-1095); d-d': m1'in çiğneme yüzeyi ve dış yüzden görünümü (A-1096, holotip); e-e': m2'nin çiğneme yüzeyi ve onun aşınmadan önceki muhtemel deseni (A-1098) f-f': m3'ün çiğneme yüzeyi ve dış yüzden görünümü (A-1099).

and *H. anatolicus* with other spalacids are not resolved; they appear as basal taxa in the same way as the outgroup taxa. The cladogram generates several monophyletic groups in particular at the nodes 4, 9 and 10.

Node 4 groups the species referred to the genera *Sinapospalax*, *Pliospalax* and *Spalax*. It is based on five synapomorphic characters (see Appendix 2): the lack of posterior arm of hypoconid (character state 10-1) and rounded anterior shape on the m1 (18-1), protosinusid reduced to an enamel island on the m2 (23-1), M1's metalophule posteriorly directed (32-1), and the protolophule of the M2 connected to the labial anteroloph (40-1).

Node 9 distinguishes *Sinapospalax marmarensis* from the other species of this genus which are grouped with *Pliospalax* and *Spalax*. Three synapomorphic characters are noted: lingual anterolophid reduced or lost on m2 (character state 20-1 & 2), protosinusid absent on m3 (27-1), and the lack of the paracone posterior spur on M1 (35-1). In this cladogram, *S. marmarensis* appears as the sister group of all other spalacids grouped in the genera *Sinapospalax, Pliospalax* and *Spalax*. We also have to note that the relationships between the species of *Sinapospalax* are not resolved.

Node 10 groups all the species referred to *Pliospalax* and *Spalax*. These are eleven apomorphic characters related to this node, of which the most characteristic are: anteroconid and metaconid fused on m1(character state 2-2), anteriorly directed and shallow protosinusid (14-1 and 17-1) on m1, S-shaped occlusal pattern of m3 (26-1), metalophule connected exclusively to the posteroloph on M1 and M2 (32-2 and 43-1, respectively), lost of anterosinus on M3 (51-2).

In the following steps, there is a gradual phylogenetic relationship from one species to another. There is no particular synapomorphy to distinguish species referred to *Spalax* from *Pliospalax*.

The present cladogram confirms the phylogenetic order between the spalacid genera already suggested by the cladistic analysis given by Sarıca and Şen (2003). However, the previous study only concerned the genera, while at the present analysis we tried to enlighten phylogenetic relationships at the species level.

BIOSTRATIGRAPHY AND PALEOENVIRONMENT

The record of fossil spalacids considerably increased during the last two decades, in particular in Turkey and Greece (Table 3). Their remains belong to four genera, and more than fifteen species have been described from some 30 localities; in addition, the occurrence of spalacids has been mentioned under various names in the preliminary faunal lists of many other mammal localities in Turkey (see Sinckenberg et al., 1975; Saraç, 2004). In other terms, spalacids are among the common elements of Neogene mammalian faunas in Turkey, and, to some extent, in the surrounding countries. The present study shows that their evolution during that period is not less dynamic than that of other rodent groups. Consequently, the spalacids may well be used as marker fossils to date Neogene terrestrial deposits.

Table 3 resumes the dispersal in time and space of the known genera and species from some key mammal localities. The earliest genus *Debruijnia* is restricted to the Early Miocene. From the early Middle Miocene upward, the genus *Sinapospalax* generates several species with some graduation in their evolutionary trends. For instance, the Middle Miocene species *S. marmarensis, S. primitivus* and *S. berdikensis* have more primitive dental features than their Late Miocene successors. From the second part of the Late Miocene, the genus *Pliospalax* develops a more lophodont dentition and spreads on a large territory covering southeastern Europe and Anatolia. The genus *Spalax* appears in late Early Pliocene (MN15). The limited time span of these genera and species provides reliable stratigraphic criteria to date Neogene terrestrial deposits.

All extant spalacids are adapted to fossorial and subterranean way of life in tubular burrows, and thus they have lost sight. How did their fossil ancestors live? The fossorial and subterraneous mode of life leads to some modifications on the body shape, limb bone anatomy, skull
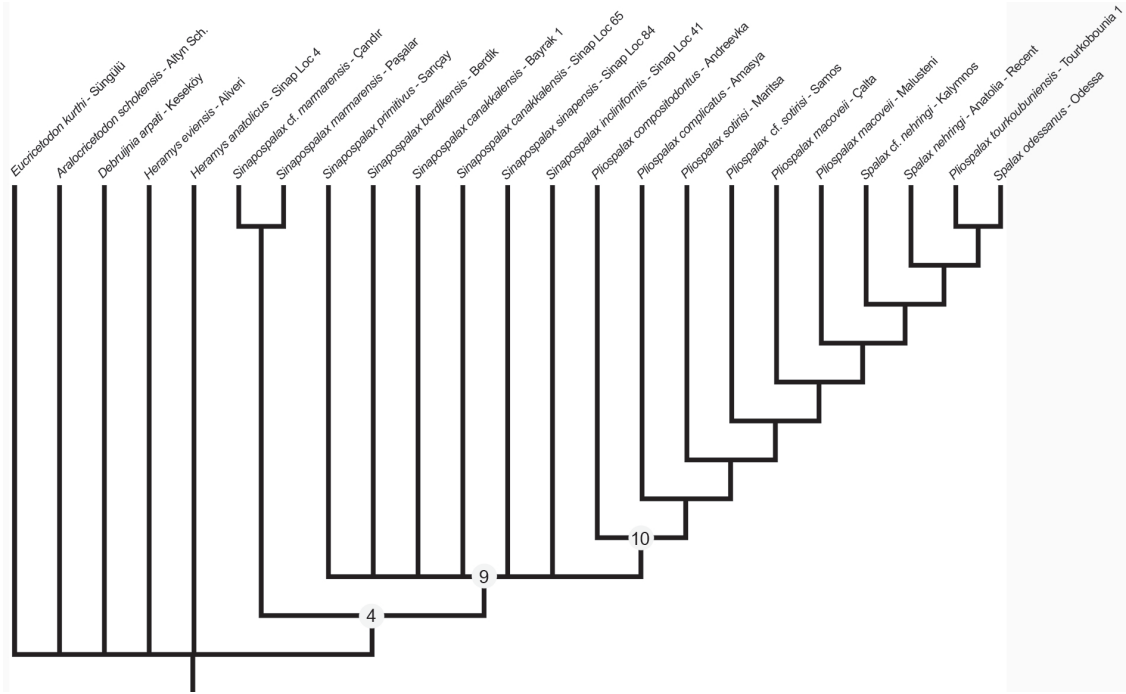
Figure 12. Cladogram illustrating the relationships among the species referred to the genera Debruijnia, Heramys, Sinapospalax, Pliospalax and Spalax, in addition to the outgroup taxa Eucricetodon kurthi and Aralocricetodon schokensis. Tree length = 212, CI = 0.618 and RI = 0.7.

Şekil 12.   Spalacidae ailesine giren Debruijnia, Heramys, Sinapospalax, Pliospalax ve Spalax cinslerine ait türlerin kladistik analiz metodu ile elde edilen evrimsel bağları. Aile dışı türler Eucricetodon kurthi ve Aralocricetodon schokensis karşılaştırma amacıyla seçilmiştir

structures and dentition. For instance, the extant mole rats have a roll-shaped body, short legs with laterally enlarged humerus, strong claws and incisors, broad rostrum and triangular-shaped braincase. Most fossil spalacids are known only from isolated molars, thus the above mentioned characters cannot be used to evaluate their degree of adaptation to the subterranean way of life. What can the dentition suggest about their behavior?

The dentition of Spalacidae displays three different patterns consequent in time. The oldest spalacid *Debruijnia* and to some extent *Heramys* have rather bunodont molars. The cusps are still well defined, and the lophs are generally lower than the cusps on unworn molars. In addition, the molars are rather brachydont or mesodont (crown height/length<1). This tooth pattern is clearly inherited from a muroid ancestor. Such a dentition is indicative of species generally inhabiting bushy wet environments and feeding on fruits and graminaceae.

The genus *Sinapospalax* first occurs in early Middle Miocene (MN5) with *S. marmarensis,* and survives till early Late Miocene (MN10). Its dentition is clearly more robust than that of *Debruijnia* and *Heramys*. The molars become more and more hypsodont, in particular in its Late Miocene representatives. In this genus, the cusps of molars are still visible in early stages of attrition, but they get progressively, with wear, included in the thick lophs. The lophs are as high as the cusps, but thinner than in the more recent genera *Pliospalax* and *Spalax*. This type of dentition is clearly adapted to a mixed feeding on graminaceae as well as roots and rhizomes. According to Flynn (2009: 143) "the robust dentaries suggest that these muroids were proodont burrowers". Spalacids became apparently adapted to subterranean life soon after the Middle Miocene climatic shift. The transition from a subtropical to generally temperate environment may have favored some groups of rodents to adapt to "an underground ecotype… with shelter from extreme climatic fluctuations

Table 3.   Chart showing the stratigraphic and geographic distribution of Mio-Pliocene Spalacidae from the main localities of which a reliable amount of material was recorded and described (modified after Ünay 1999; Sarıca and Şen, 2003). The chronology of Sinap Tepe localities (Locs.) are taken from Kappelman et al., 2003. The species described in the present study are indicated by bold characters.

Tablo 3.   Miyosen ve Pliyosen Spalacidae ailesi türlerinin yatay ve dikey dağılımı (Ünay, 1999 ve Sarıca ve Şen, 2003'deki verilerinden değiştirilmiş ve çoğaltılmıştır). Sinap Tepe lokalitelerinin kronolojisi Kappelman ve diğ. (2003)'e göredir. Bu yayında tanımlanan türler koyu renkli harflerle yazılıdır.

MN ZONES	Ukraine, Romania, Bulgaria	Greece	Turkey
16		*P. tourkobouniensis* (Tourkobounia-1)	
15	*Spalax odessanus* (Kotlovina) (Odessa Catacombes) *Pliospalax macovei* (Malusteni, Beresti, Muselievo)	*Spalax odessanus* (Karaburun)	*P. macovei* (Çalta)
14	*P. macovei* (Krashnopol, Frunzovka-1)	*P. sotirisi* (Maritsa)	*Pliospalax* n. sp. (İğdeli)
13	*Pliospalax compositodontus* (Andreevka,16th Station,		***Pliospalax complicatus* n. sp., Amasya**
12	*P.* sp. (Novoelizavetovka 3)	*Pliospalax* cf. *sotirisi* (Samos)	*Pliospalax* n.sp. 4 (Düzyayla-1) *Pliospalax* n.sp. 3 (Düzyayla-1)
11			
10			*Sinapospalax sinapensis* (Sinap Tepe Loc. 84)
9			*Sinapospalax* n.sp. (Sinap Loc. 12) *Sinapospalax incliniformis* (Sinap Loc. 41) *Sinapospalax* sp. 1 & 2 (Sinap Loc. 41) ***Sinapospalax sp.* (Sinap Loc. 120, Direcik-1)** *Heramys anatolicus* (Sinap Loc. 4)
8 + 7 6			*Sinapospalax* n. sp. (Pişmanköy) *Sinapospalax canakkalensis* (Bayraktepe-1, Yeni Eskihisar, Sinap Loc. 65) *Sinapospalax primitivus* (Sarıçay) ***Sinapospalax berdikensis* n. sp. (Berdik-1)** *Sinapospalax* cf. *marmarensis* (Çandir)
5			*Sinapospalax marmarensis* (Paşalar)
4		*Heramys eviensis* (Aliveri)	*Debruijnia* n. sp. (Dededağ, Söke)
3			*Debruijnia arpati* (Keseköy, Sabuncubeli)

and predators" as noted by Ünay (1999: 42). The increasing hypsodonty and lophodonty in the dentition of late Middle Miocene and Late Miocene Spalacidae seems to be the morphologic reply of the dentition to the animals' progressive adaptation to the subterraneous life.

CONCLUSIONS

The two new species described from the Middle and Late Miocene of southwestern Anatolia fill some gaps in the stratigraphic distribution of spalacids in Turkey. This study confirms once more that the spalacids are among the common elements of Neogene rodent faunas in Turkey, at least after the Middle Miocene. Until today, ten named species referred to the fossil genera *Debruijnia*, *Heramys*, *Sinapospalax* and *Pliospalax* have been recorded in Turkey from the Early Miocene to the Pliocene. In addition to the list of key localities given in Table 3 and Appendix 1, the spalacids are known in Turkey from some twenty other Neogene localities (Sickenberg et al. 1975; Sarıca and Şen 2003; Saraç 2004). Their abundance in the fossil record shows once more that this family generated a great diversity all through its history in Turkey, as its living representatives are doing today. The richness of the fossil record and the speciation dynamics of this family result in their use as a reliable biochronologic tool for terrestrial Neogene deposits in Turkey.

The fossil species of Spalacidae are grouped in five genera based on their dental features. We intended to check the validity of systematic assignments through a parsimony analysis of the morphological features of their molars. The results show that the genera *Debruijnia* and *Heramys* from the Early Miocene appear as undistinguished basal groups. The species of the genera *Sinapospalax*, *Pliospalax* and *Spalax* show a gradual phylogenetic relationship from one species to another. There is no particular synapomorphy to distinguish species referred to *Spalax* from *Pliospalax*, which are grouped in the same clade.

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Appendix 1. Selected outgroup and ingroup species for phylogenetic analysis of Spalacidae.

Ek 1. Spalacidae ailesinin filojeni analizi için dikkate alınan aile dışı (outgroup) ve aile içi (ingroup) türlerin listesi.

Eucricetodon (Atavocricetodon) kurthi de Bruijn et al., 2003 from Süngülü, northeastern Turkey, Eocene/Oligocene boundary, outgroup species

Aralocricetodon schokensis Bendukidze, 1993 from Altyn Schokysu, Kazakhstan, Late Oligocene, after Lopatin 2004 and Bendukidze et al. 2009, outgroup species

Debruijnia arpati Ünay, 1996 from Keseköy, Turquie, MN3

Heramys eviensis Klein Hofmeijer and de Bruijn, 1985 from Aliveri, Evia Island, Greece, MN4

Heramys anatolicus Sarıca and Şen 2003 from Sinap Tepe Loc. 4, Turkey, MN9

Sinapospalax marmarensis (Ünay, 1990) from Pasalar, Turkey, MN5/6

Sinapospalax cf. *marmarensis* from Çandir, Turkey, MN 6, after de Bruijn et al. 2003

Sinapospalax primitivus (Ünay, 1978) from Sariçay, Turkey, MN7/8

Sinapospalax canakkalensis (Ünay, 1981) from Bayraktepe-1, Turkey, MN7/8

Sinapospalax canakkalensis from Sinap Tepe Loc. 65, Turkey, MN8, after Sarıca and Şen 2003

Sinapospalax berdikensis n. sp. from Berdik-1, Turkey, MN7/8

Sinapospalax sinapensis Sarıca and Şen, 2003 from Sinap Tepe Loc. 84, Turkey, MN9

Sinapospalax incliniformis Sarıca and Şen, 2003 from Sinap Tepe Loc. 41, Turkey, MN9

Pliospalax complicatus n. sp. from Amasya, Turkey, MN13

Pliosplax compositodontus Topachevski, 1969 from Andreevka, Ukraine, Late Meotian.

Pliosplax sotirisi de Bruijn et al., 1970 from Maritsa, Rhodes Island, Greece, MN14

Pliosplax cf. *sotirisi* from Mytilini B, Samos Island, Greece, MN12, after Black et al., 1980 and Vasileiadou and Sylvestrou, 2009

Pliosplax macoveii (Simionescu, 1930) from Malusteni, Romania, MN15, after Topachevski, 1969

Pliosplax macoveii from Çalta, Turkey, MN15, after Şen 1977

Pliosplax tourkobouniensis de Bruijn and van der Meulen, 1975 from Tourkobounia-1, Greece, MN16

Spalax odessanus Topachevski, 1969 from Odessa Catacombes, Ukraine, MN15

Spalax nehringi (Satunin, 1898) from Anatolia, Recent, after Topachevski 1969

Spalax cf. *nehringi* from Kalymnos Island, Greece, Early Biharian, after Kuss & Storch 1978

Appendix 2. List of characters and their states presented in the data matrix of Appendix 3. The character analysis was principally based on fresh teeth; in case of all specimens are worn teeth, we tried to reconstruct their fresh state, at least for some key characters, in comparison with their equivalents in other species.

Ek 2. *Ek 3'deki tabloda verilen diş özellikler-*
inin ve bu özelliklerin çeşitli safhalarının listesi.
Diş özellillerinin analizi genellikle aşınmamış
veya az aşınmış dişler üzerinde yapıldı. Eğer bir
lokalitedeki bütün örnekler aşınmış dişler ise,
bazı anahtar özellikler başka türlerdeki benzer
dişlerle karşılaştırılarak belirlenmeye çalışıldı.

1. m1 anteroconid situated

　　　0: central; 1: labial

2. m1 anteroconid-metaconid (Fig. 7)

　　　0: separated; 1: connected by a lophid;
　　　2: fused forming a lophid

3. m1 anteroconid-metaconid size (Fig. 7)

　　　0: almost equal in size; 1: metaconid
　　　strikingly bigger

4. m1 protoconid-metaconid

　　　0: connected by posterior metalo-
　　　phulid; 1: not connected

5. m1 protoconid connected to anteroconid by

　　　0: anterolophulid; 1: labial anterolo-
　　　phid; 2: not connected

6. m1 mesolophid

　　　0: present; 1: absent

7. m1 mesolophid

　　　0: well developed; 1: weak

8. m1 labial anterolophid

　　　0: distinct; 1: fused to protoconid

9. m1 anterolophulid

　　　0: complete; 1: fragmented or absent

10. m1 posterior arm of hypoconid

　　　0: present; 1: absent

11. m1 ectomesolophid

　　　0: present; 1: absent

12. m1 posterosinusid

　　　0: open; 1: closed

13. m1 protosinusid

　　　0: present; 1: absent

14. m1 protosinusid

　　　0: rather transverse; 1: anteriorly di-
　　　rected

15. m1 sinusid depth (vertical) (Fig. 8)

　　　0: shallow; 1: deep

16. m1 sinusid orientation

　　　0: rather transverse; 1: posteriorly di-
　　　rected

17. m1 depth of protosinusid (Fig. 8)

　　　0: deep; 1: shallow

18. m1 anterior shape of tooth

　　　0: rather sharp; 1: rather rounded

19. m2 occlusal pattern (Fig. 9-I)

　　　0: cricetid pattern; 1: S shaped

20. m2 lingual anterolophid (Fig. 9-III)

　　　0: long; 1: short; 2: absent

21. m2 mesolophid

　　　0: strong; 1: weak or absent

22. m2 protosinusid

　　　0: present; 1: absent

23. m2 protosinusid

　　　0: open; 1: enamel island

24. m2 sinusid orientation

　　　0: transverse; 1: posteriorly

25. m2 posterosinusid occurrence

　　　0: open; 1: enamel island

26. m3 occlusal pattern

　　　0: cricetid pattern; 1: S-shaped

27. m3 protosinusid

　　　0: present; 1: absent

28. m3 protosinusid

　　　0: open; 1: enamel island

29. m3 sinusid orientation

　　　0: transverse; 1: posteriorly

30. m3 anterosinusid occurrence

　　　0: present; 1: absent

31. M1 metacone

    0: not isolated; 1: isolated

32. M1 metalophule orientation (Fig. 5-I)

    0: directed to hypocone; 1: directed to posterior arm of hypocone; 2: directed to posteroloph

33. M1 mesoloph

    0: strong; 1: short; 2: absent

34. M1 anterior arm of protocone

    0: present; 1: absent

35. M1 paracone posterior spur

    0: present; 1: absent

36. M1 protolophule (Fig. 5-I)

0: rather transverse; 1: posteriorly directed

37. M1 protosinus occurrence

    0: deep; 1: reduced; 2: depression state; 3: absent

38. M1 sinus orientation

    0: rather transverse; 1: anteriorly directed; 2: L shaped

39. M2 paracone

    0: labial to protocone; 1: shifted anteriorly; 2: incorporated into anteroloph

40. M2 protolophule

    0: connected to protocone; 1: connected to labial anteroloph; 2: fused with labial anteroloph and anterosinus lost

41. M2 occlusal pattern (Fig. 6-I)

    0: cricetid type; 1: S-shaped

42. M2 mesoloph

    0: reaches the labial border; 1: stays in the area of mesosinus; 2: absent

43. M2 metalophule

    0: distinct loph; 1: fused with posteroloph

44. M2 metalophule orientation

    0: transverse; 1: posteriorly

45. M2 ectoloph between anteroloph and paracone

    0: absent; 1: present

46. M2 paracone posterior spur

    0: absent; 1: present

47. M2 posterosinus

    0: well developed; 1: weak; 2: absent

48. M3 protocone-hypocone connection

    0: connected; 1: not connected

49. M3 protocone-hypocone connection

    0: with central endoloph; 1: with lingual endoloph

50. M3 lingual anteroloph

    0: present; 1: absent

51. M3 anterosinus

    0: open; 1: enclosed by anteroloph and paracone; 2: absent

52. M3 number of labial sinus

    0: four to three; 1: three to two; 2: two to one

53. loph and cone relation

    0: all cones recognizable, lophs weak; 1: all cones recognizable, lophs strong; 2: cones included in lophs

54. crown height of M1, M2, m1, m2

    0: brachydont (L>H); 1: mesodont: (L=H); 2: rather hypsodont: (L<H)

55. crown height of upper molars

    0: labially and lingually equal; 1: lingually high;

56. sinus(id)s width

    0: wide; 1: narrow

57. M1 and m1 anterocone(id) shape

    0: distinct cone; 1: retracted loph-like; 2: included completely in the anterior loph

58. loph(id) height

    0: lower than cone(id) height; 1: equal to cone(id) height.

Appendix 3. Character state matrix for species of Spalacidae and outgroup taxa E. kurthi and A. schokensis. (?) means the character cannot be observed, (-) means that the character does not concern the species.

Ek 3. Spalacidae ailesi türlerinin ve aile dışı (outgroup: E. kurthi ve A. schokensis) iki türün kotlanmış özelliklerinin listesi. (?) malzeme yetersizliği nedeniyle gözlenemeyen, (-) bir türde olmayan özellikleri işaret eder.

Species-Localities / Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Eucricetodon kurthi-Süngülü	0	0	1	0	2	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Aralocricetodon schokensis-Kazak	0&1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Debrujinia arpati-Keseköy	0	1	0	0&1	0	0	0	0	0&1	0	0	0	0	1	1	0&1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Heramys eviensis-Aliveri	1	1	1	1	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0
Heramys anatolicus-Sinap Loc 4	1	1	1	1	0	0	0	0	0	1	1	0	0	1	1	0	0	0	1	?	0	?	?	1	?	1	0	1	0&1	0
Sinapospalax marmarensis-Pasalar	1	1	1	1	0&2	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	1	0
S. cf. marmarensis-Çandir	1	1	1	0	0	0	0	0	0	?	1	0	0	0	1	1	0	?	0	0	0	0	1	1	0	0	0	1	0&1	0
Sinapospalax primitivus-Sariçay	1	1	1	1	0	0	0	0	0&1	1	1	0	0	0	1	0&1	0	1	0&1	1	0	?	-	1	1	1	1	-	0	0
Sinapospalax berdikensis-Berdik-1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	-	0	0
S. canakkalensis-Bayraktepe I	1	1	1	1	0&2	0	0	0	1	1	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	?	?	?	?	?
Sinapospalax canakkalensis-Loc 65	1	1	1	1	2	0	0	0	1	1	1	0	0	0	1	1	0	1	0	1	0	0	1	1	0&1	0	1	-	1	0
Sinapospalax sinapensis-Loc 84	1	1	1	1	0	0	0	0	0&1	1	1	0	0	0	1	1	0	1	1	0	0&1	0	1	1	0	0	0	1	0	0
Sinapospalax incliniformis-Loc 41	1	2	1	1	2	0	0	0	1	1	1	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	0	0
Pliospalax complicatus-Amasya	1	2	1	1	0	0	0	0	0&1	1	1	0	0	1	1	1	0	1	0	?	0	?	?	1	0	1	1	-	0	1
P. compositodontus-Andreevka	1	2	1	1	0	0	0	?	0	1	1	0	0	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Pliospalax cf. sotirisi-Samos	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0&1	2	1	0	1	1	0	0	0	1	0	0

Species-Localities / Characters	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
*Pliospalax sotirisi-*Maritsa	1	2	1	1	0	1	1	0	0	1	0	0	1	1	1	1	1	0&1	1	0	1	1	0	?	?	?	?	?
*Pliospalax macoveii-*Malusteni	1	2	1	1	0&1	1	1	0	0	1	0	0	?	1	1	1	1	0&1	1	1	-	1	1	1	1	-	1	1
*Pliospalax macoveii-*Çalta	1	2	1	1	0&1	1	1	0&1	0	1	0	0	1	1	1	1	1	0&1	1	1	1	1	0&1	1	0	1	1	0
*P. tourkobouniensis-*Tourkobounia	1	2	1	1	0&1	1	?	1	1	1	0	0&1	-	1	1	1	1	2	1	1	1	0&1	1	1	1	-	0	1
*Spalax odessanus-*Odessa	1	2	1	1	0&1	1	-	1	1	1	1	1	-	1	-	-	1	2	1	1	-	1	1	1	1	-	1	1
Spalax cf. *nehringi-*Kalymnos	0	2	1	1	0	1	-	1	0	0	1	0	1	1	1	1	1	2	1	1	1	1	1	1	1	-	1	1
*Spalax nehringi-*Anatolia	0	2	1	1	0	1	-	1	0	1	1	1	-	1	-	-	1	2	1	1	-	1	1	1	1	-	1	1
*Eucricetodon kurthi-*Süngülü	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0&1	0	0	0	0	0	0	0	0
*Aralocricetodon schokensis-*Kazak	0	1	1	1	0	0	0	0	0	0	0	1	0	0&1	0	1	0	0	0	1	0&1	0	0	0&1	1	0	0	0
*Debrujinia arpati-*Keseköy	0	0	0&1	0	0	0	0	1	0	0	0	0	0	0&1	0	0	1	0	0&1	1	0	0	0&1	1	1	0&1	0	0
*Heramys eviensis-*Aliveri	0	0	0&1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
*Heramys anatolicus-*Sinap Loc 4	?	?	?	?	?	?	?	?	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
*Sinaposplax marmarensis-*Pasalar	0	1	1	1	0	0	2	1	1	0&1	0	0	0	1	0	0	0	0	1	1	0&1	0	1	2	1	1	1	1
*S.*cf *marmarensis-*Çandir	0	1	0	0	0	0&1	2	1	0&1	0&1	0	0	0	1	0&1	1	0	1	-	1	1	1	1	2	1	1	1	1
*Sinapospalax primitivus-*Sariçay	0	1	0&1	1	1	0	2	1	0	0&1	0	0	1	1	1	1	2	0&1	1	1	1	0	1	2	1	1	1	1
*Sinapospalax berdikensis-*Berdik	0	1	1	1	1	0	3	2	0	0	0	0&1	0	1	0	1	1	1	-	1	1	1	1	2	2	1	2	2
*S. canakkalensis-*Bayraktepe I	1	1	0&1	1	0&1	0	2	1&2	0&1	0&1	0	0	0	1	0	1	0	1	-	1	1	1	1	2	1	1	1	1

Taxon	Character states
S. canakkalensis-Loc 65	1 1 1 1 1 1 1 0 0 0 1 0 1 0 0 2 2 0 1 0 0 0 1 0 0 0 0 1 1 2 1 1 1 1 1 1 1 1 1 1
Sinapospalax sinapensis-Loc 84	0 1 ? ? 1 0&1 ? 2 ? 1 1 1
Sinapospalax incliniformis-Loc 41	? ? ? ? 1 ? 2 ? 1 2 1
Pliospalax complicatus-Amasya	0 1 2 1 1 1 3 1 0&1 1 0 0 1 1 ? 1 1 1 1 1 0 0 0 0 ? ? ? ? ? 1 0&1 1 1 2 1 2 1 1 1&2 1
P. composidontus-Andreevka	0 2 0&1 1 1 0 2 1 1 1&2 1 1 0 0 1 0 0 1 1 ? 1 2 1 2 1 – 1 2 1 1 1 ? 1 1 2 1 ? 2 2 1
Pliospalax cf. sotirisi-Samos	0 2 1 1 1 1 3 1 0&1 2 1 1 0 1 1 0 1 1 1 1 1 2 1 2 1 1 1 2 1 2 2 2 2 2 2 2 1 2 2 1
Pliospalax sotirisi-Maritza	0 2 1 1 1 0 3 1 0 2 0 0 1 1 1 0 1 1 1 1 1 2 1 2 1 1 1 2 1 2 2 2 2 2 2 2 1 2 2 1
Pliospalax macoveii-Malusteni	0 2 1 1 1 1 3 1 2 0&1 0 1 1 1 1 0 1 1 1 1 1 2 1 2 1 1 1 2 1 2 2 2 2 2 2 2 ? 2 2 1
Pliospalax macoveii-Çalta	0 2 1 1 1 1 3 1 2 0&1 1 1 1 1 1 0 1 1 1 1 1 2 1 2 1 1 1 2 1 2 2 2 2 2 2 2 1 2 2 1
P. tourkobouniensis-Tourkob	0 2 1 1 1 0 3 1 2 0 2 1 1 1 1 0 1 1 1 1 1 2 1 2 1 1 1 2 1 2 2 2 2 2 2 1 1 2 2 1
Spalax odessanus-Odessa	0 2 1 1 1 0 3 1 2 1 2 1 1 1 1 0 1 ? ? 1 ? 2 ? 2 2 1 2 2 ? 2 1 0 2 2 2 2 1 2 2 1
Spalax cf. nehringi-Kalymnos	0 2 1 1 1 1 3 1 2 1 2 1 1 1 1 0 1 1 ? 1 1 2 2 2 2 1 2 2 ? 2 1 0 2 2 2 2 ? 2 2 1
Spalax nehringi-Anatolia	0 2 1 1 1 0 3 1 2 1 2 1 1 1 1 0 1 1 1 1 1 2 2 2 2 1 2 2 1 2 1 0 2 2 2 2 1 2 2 1